HARVARD UNIVERSITY

LIBRARY

OF THE

Museum of Comparative Zoology

UNIVERSITY OF KANSAS PUBLICATIONS
MUSEUM OF NATURAL HISTORY

6041-21
Batt.

VOLUME 15 · 1961-1966

EDITORS

E. RAYMOND HALL, *Chairman*
THEODORE H. EATON, JR.
HENRY S. FITCH
FRANK B. CROSS

MUSEUM OF NATURAL HISTORY
UNIVERSITY OF KANSAS
LAWRENCE
1966

-NA-L

MUSEUM OF NATURAL HISTORY
UNIVERSITY OF KANSAS
LAWRENCE

PRINTED BY
ROBERT R. (BOB) SANDERS, STATE PRINTER
TOPEKA, KANSAS
1966

31-4589

CONTENTS OF VOLUME 15

1. The amphibians and reptiles of Michoacán, México. By William E. Duellman. Pp. 1-148, pls. 1-6, 11 figs. December 20, 1961.
2. Some reptiles and amphibians from Korea. By Robert G. Webb, J. Knox Jones, Jr., and George W. Byers. Pp. 149-173. January 31, 1962.
3. A new species of frog (genus Tomodactylus) from western México. By Robert G. Webb. Pp. 175-181, 1 fig. March 7, 1962.
4. Type specimens of amphibians and reptiles in the Museum of Natural History, The University of Kansas. By William E. Duellman and Barbara Berg. Pp. 183-204. October 26, 1962.
5. Amphibians and reptiles of the rainforests of southern El Petén, Guatemala. By William E. Duellman. Pp. 205-249, pls. 7-10, 6 figs. October 4, 1963.
6. A revision of snakes of the genus Conophis (family Colubridae, from Middle America). By John Wellman. Pp. 251-295, 9 figs. October 4, 1963.
7. A review of the Middle American tree frogs of the genus Ptychohyla. By William E. Duellman. Pp. 297-349, pls. 11-18, 7 figs. October 4, 1963.
8. Natural history of the racer Coluber constrictor. By Henry S. Fitch. Pp. 351-468, pls. 19-22, 20 figs. December 30, 1963.
9. A review of the frogs of the Hyla bistincta group. By William E. Duellman. Pp. 469-491, 4 figs. March 2, 1964.
10. An ecological study of the garter snake, Thamnophis sirtalis. By Henry S. Fitch. Pp. 493-564, pls. 23-25, 14 figs. May 17, 1965.
11. Breeding cycle in the ground skink, Lygosoma laterale. By Henry S. Fitch and Harry W. Greene. Pp. 565-575, 3 figs. May 17, 1965.
12. Amphibians and reptiles from the Yucatan Peninsula, México. By William E. Duellman. Pp. 577-614, 1 fig. June 22, 1965.
13. A new species of turtle, genus Kinosternon, from Central America. By John M. Legler. Pp. 615-625, pls. 26-28, 2 figs. June 20, 1965.
14. A biogeographic account of the herpetofauna of Michoacán, México. By William E. Duellman. Pp. 627-709, pls. 29-36, 5 figs. December 30, 1965.
15. Amphibians and reptiles of Mesa Verde National Park, Colorado. By Charles L. Douglas. Pp. 711-744, pls. 37, 38, 6 figs. March 7, 1966.

Index, pp. 745-770.

UNIVERSITY OF KANSAS PUBLICATIONS
MUSEUM OF NATURAL HISTORY

Volume 15, No. 1, pp. 1-148, pls. 1-6, 11 figs.
December 20, 1961

MUS. COMP. ZOOL.
LIBRARY
FEB 21 1962
HARVARD
UNIVERSITY

The Amphibians and Reptiles of Michoacán, México

BY

WILLIAM E. DUELLMAN

UNIVERSITY OF KANSAS
LAWRENCE
1961

UNIVERSITY OF KANSAS PUBLICATIONS
MUSEUM OF NATURAL HISTORY

Institutional libraries interested in publications exchange may obtain this series by addressing the Exchange Librarian, University of Kansas Library, Lawrence, Kansas. Copies for individuals, persons working in a particular field of study, may be obtained by addressing instead the Museum of Natural History, University of Kansas, Lawrence, Kansas. There is no provision for sale of this series by the University Library, which meets institutional requests, or by the Museum of Natural History, which meets the requests of individuals. However, when individuals request copies from the Museum, 25 cents should be included, for each separate number that is 100 pages or more in length, for the purpose of defraying the costs of wrapping and mailing.

* An asterisk designates those numbers of which the Museum's supply (not the Library's supply) is exhausted. Numbers published to date, in this series, are as follows:

Vol. 1. Nos. 1-26 and index. Pp. 1-638, 1946-1950.

*Vol. 2. (Complete) Mammals of Washington. By Walter W. Dalquest. Pp. 1-444, 140 figures in text. April 9, 1948.

Vol. 3. *1. The avifauna of Micronesia, its origin, evolution, and distribution. By Rollin H. Baker. Pp. 1-359, 16 figures in text. June 12, 1951.

*2. A quantitative study of the nocturnal migration of birds. By George H. Lowery, Jr. Pp. 361-472, 47 figures in text. June 29, 1951.

3. Phylogeny of the waxwings and allied birds. By M. Dale Arvey. Pp. 473-530, 49 figures in text, 13 tables. October 10, 1951.

4. Birds from the state of Veracruz, Mexico. By George H. Lowery, Jr., and Walter W. Dalquest. Pp. 531-649, 7 figures in text, 2 tables. October 10, 1951.

Index. Pp. 651-681.

*Vol. 4. (Complete) American weasels. By E. Raymond Hall. Pp. 1-466, 41 plates, 31 figures in text. December 27, 1951.

Vol. 5. Nos. 1-37 and index. Pp. 1-676, 1951-1953.

*Vol. 6. (Complete) Mammals of Utah, *taxonomy and distribution*. By Stephen D. Durrant. Pp. 1-549, 91 figures in text, 30 tables. August 10, 1952.

Vol. 7. *1. Mammals of Kansas. By E. Lendell Cockrum. Pp. 1-303, 73 figures in text, 37 tables. August 25, 1952.

2. Ecology of the opossum on a natural area in northeastern Kansas. By Henry S. Fitch and Lewis L. Sandidge. Pp. 305-338, 5 figures in text. August 24, 1953.

3. The silky pocket mice (Perognathus flavus) of Mexico. By Rollin H. Baker. Pp. 339-347, 1 figure in text. February 15, 1954.

4. North American jumping mice (Genus Zapus). By Philip H. Krutzsch. Pp. 349-472, 47 figures in text, 4 tables. April 21, 1954.

5. Mammals from Southeastern Alaska. By Rollin H. Baker and James S. Findley. Pp. 473-477. April 21, 1954.

6. Distribution of Some Nebraskan Mammals. By J. Knox Jones, Jr. Pp. 479-487. April 21, 1954.

7. Subspeciation in the montane meadow mouse. Microtus montanus, in Wyoming and Colorado. By Sydney Anderson. Pp. 489-506, 2 figures in text. July 23, 1954.

8. A new subspecies of bat (Myotis velifer) from southeastern California and Arizona. By Terry A. Vaughan. Pp. 507-512. July 23, 1954.

9. Mammals of the San Gabriel mountains of California. By Terry A. Vaughan. Pp. 513-582, 1 figure in text, 12 tables. November 15, 1954.

10. A new bat (Genus Pipistrellus) from northeastern Mexico. By Rollin H. Baker. Pp. 583-586. November 15, 1954.

11. A new subspecies of pocket mouse from Kansas. By E. Raymond Hall. Pp. 587-590. November 15, 1954.

12. Geographic variation in the pocket gopher, Cratogeomys castanops, in Coahuila, Mexico. By Robert J. Russell and Rollin H. Baker. Pp. 591-608. March 15, 1955.

13. A new cottontail (Sylvilagus floridanus) from northeastern Mexico. By Rollin H. Baker. Pp. 609-612. April 8, 1955.

14. Taxonomy and distribution of some American shrews. By James S. Findley. Pp. 613-618. June 10, 1955.

15. The pigmy woodrat, Neotoma goldmani, its distribution and systematic position. By Dennis G. Rainey and Rollin H. Baker. Pp. 619-624, 2 figures in text. June 10, 1955.

Index. Pp. 625-651.

(Continued on inside of back cover)

University of Kansas Publications
Museum of Natural History

Volume 15, No. 1, pp. 1-148, pls. 1-6, 11 figs.
December 20, 1961

The Amphibians and Reptiles of Michoacán, México

BY

WILLIAM E. DUELLMAN

University of Kansas
Lawrence
1961

University of Kansas Publications, Museum of Natural History
Editors: E. Raymond Hall, Chairman, Henry S. Fitch,
Theodore H. Eaton, Jr.

Volume 15, No. 1, pp. 1-148, pls. 1-6, 11 figs.
Published December 20, 1961

University of Kansas
Lawrence, Kansas

MUS. COMP. ZOOL.
LIBRARY
FEB 21 1962
UNIVERSITY

PRINTED IN
THE STATE PRINTING PLANT
TOPEKA, KANSAS
1961
28-7817

The Amphibians and Reptiles of Michoacán, México

BY

WILLIAM E. DUELLMAN

CONTENTS

PAGE

Introduction 3
Acknowledgments 5
Historical Account 7
Natural Landscape 9
Geography of the Herpetofauna 13
Annotated List of Species 13
Amphibia 14
Caudata 14
Salientia 20
Reptilia 56
Testudines 56
Crocodilia 58
Sauria 59
Serpentes 88
Species of Questionable Occurrence 124
Gazetteer 129
Summary 141
Literature Cited 142

INTRODUCTION

For almost 30 years North American herpetologists have been making extensive collections of reptiles and amphibians in México. Some parts of the country, because of their accessibility, soon became relatively well known; other regions lying off the beaten path were bypassed or inadequately sampled. Principally in the last decade herpetologists have been entering regions from which no collections previously were available in an attempt to fill gaps in known distributions and to discover unknown species of animals. In 1950 Dr. Donald D. Brand led an exploration party from the University of Texas to the poorly explored and faunistically unknown region of southwestern Michoacán. James A. Peters accompanied Brand and collected amphibians and reptiles. In 1951 I welcomed the opportunity to accompany Brand on a second expedition to southwestern Michoacán. Such was the beginning of my interest

in the herpetofauna of the region. I have been fortunate to return to Michoacán on four successive trips, all of which had as their purpose the accumulation of data on the herpetofauna that would result in a survey of the component species and an analysis of their distribution.

My original intention was to amplify Peters' (1954) study based on the collections made by him in 1950 and by me in 1951 in the Sierra de Coalcomán. But it soon became evident that in order to understand the relationships of the herpetofauna of the Sierra de Coalcomán, the species inhabiting the Tepalcatepec Valley and adjacent mountain ranges would have to be studied. In the course of making that study I examined all specimens from Michoacán already in museums.

There have been few detailed herpetofaunal studies in México. The first such study of any consequence was that by Bogert and Oliver (1945) on the herpetofauna of Sonora. In that paper the authors analyzed the fauna from a geographic view and showed the transition from tropical species in the southern part of the state to members of the Sonoran Desert assemblage to the north. Martin (1958) made a detailed study of the herpetofauna of the Gómez Farías region in southern Tamaulipas; he emphasized the ecological distribution of amphibians and reptiles in that region with special reference to cloud forests. Duellman (1958c) presented a preliminary geographic analysis of the herpetofauna of Colima with special reference to the continuity of the species inhabiting the lowlands. Zweifel (1960) discussed in detail the herpetofauna of the Tres Marías Islands and commented on the derivation of the fauna. Duellman (1960d) provided a detailed account of the geographic distribution of the amphibians known to occur in the lowlands of the Isthmus of Tehuantepec and attempted to account for the present patterns of distribution.

The present report is the first of two parts dealing with the herpetofauna of Michoacán. The purpose of this part is to present a full account of the species of amphibians and reptiles known to inhabit the state of Michoacán; the accounts of the species are accompanied by a brief description of the natural landscape and of the various assemblages of species comprising the major faunistic groups within the region. A gazetteer of collecting localities is appended. The second part of the study, now in preparation, deals with the ecological and historical geography of the herpetofauna. Since the present part will be of interest primarily to systematic

herpetologists, I have decided to separate it from the more general material of interest to biogeographers.

One of the major problems that faces the worker undertaking a faunal study is the presence of species or genera of unsettled systematic status. My work in Michoacán has been no exception; fifteen separate studies were undertaken in an attempt to solve systematic problems in certain groups. Some systematic problems still remain but are of little consequence insofar as the entire faunal picture is concerned, or are so involved as to be impractical to undertake at this time. In accounts of species, such problems are mentioned in the hope that they will interest some worker who will be inclined to investigate them.

ACKNOWLEDGMENTS

While engaged in the study of the herpetofauna of Michoacán I have built up a debt of gratitude to many individuals, without whose aid my ambition to complete my study never would have been realized. I am especially grateful to those individuals who accompanied me in the field; Lee D. Beatty, Richard E. Etheridge, Carter R. Gilbert, Fred G. Thompson, Jerome Tulecke, and John Wellman offered stimulating companionship and valuable assistance. On many occasions they suffered hardships on behalf of my interests.

Studies of my own specimens have been augmented by material from other institutions. For permitting me to examine specimens in their care I am indebted to W. Frank Blair, Charles M. Bogert, Doris M. Cochran, William B. Davis, James R. Dixon, the late Emmett R. Dunn, Josef Eiselt, Alice G. C. Grandison, Norman Hartweg, Robert F. Inger, Arthur Loveridge, the late Karl P. Schmidt, Hobart M. Smith, Robert C. Stebbins, Margaret Storey, Edward H. Taylor, and Richard G. Zweifel.

Several people have aided me in the study of specimens and in the analysis of data; I am grateful to Donald D. Brand, who first introduced me to Michoacán; since that time I have benefited much from his knowledge of the area. James A. Peters provided me with essential information concerning his field work in southern Michoacán in 1950. James R. Dixon and Floyd L. Downs have permitted me to use freely the material and data that they accumulated in their recent field work in Michoacán. Norman E. Hartweg allowed me to use the specimens and data that he gathered in his survey of the herpetofauna in the region of Volcán Parícutin. L. C. Stuart, Charles

F. Walker, and Richard G. Zweifel have helped in unraveling some of the systematic and distributional problems.

I am especially grateful to my wife, Ann, who for six months helped me track down elusive species and explore new areas. Furthermore, she has stimulated me to carry this study to completion.

Many people in Michoacán favored the field parties with quarters, transportation, and valuable information, which greatly facilitated the field work. In this respect I am especially indebted to Ingeniero Ruben Erbina of Ingenieros Civiles Asociados, who not only let us use his home as our headquarters, but through a letter of introduction gave us the "key" to southern Michoacán. Ingeniero Pedro Tonda aided us in Arteaga and San Salvador. Ingeniero Anastacio Peréz Alfaro of the Comisión Tepalcatepec in Uruapan provided the latest maps of southern Michoacán and much essential information pertaining to travel conditions in the area. Señor Nefty Mendoza gave us a home in Dos Aguas; this kindness allowed us to work in this interesting region during the height of the rainy season. Mr. and Mrs. Bob Thomas let us make use of their facilities at Hacienda Zirimicuaro. The naval officers at the Estación Marina at Playa Azul made pleasant what might have been a dreadful stay in that small coastal village. To the managers and pilots of Lineas Aereas Picho in Uruapan I owe special thanks for going out of their way on more than one occasion to transport a stranded snake-hunter. Throughout the months of field work beginning in 1955 I constantly have been aided by the authorities and workers of the Comisión Tepalcatepec, a subdivision of the Secretaria de Caminos y Obras Publicas, and of the private corporation, Ingenieros Civiles Asociados. Much of the field work in Michoacán was made possible only through the co-operation of the natives who supplied mules, acted as guides, and aided in the collection of specimens. I have learned a great deal from these people. They will never see this report. Their work as guides, muleteers, and collectors greatly assisted me with the mountains of equipment that had to be piled on the backs of scrawny mules for transportation to places where the natives seldom trod. Their efforts in behalf of Don Guillermo never will be forgotten; I extend an especially hearty *muchas gracias* to Benjamin, Ignacio, Jesús, Lorenzo, Mariano, and Remigio.

Much of the work on this report was done while I was associated with the Museum of Zoology at the University of Michigan. I thank Norman E. Hartweg and T. H. Hubbell for making available

to me the facilities of the museum and for their numerous courtesies that aided me so much.

My field work in Michoacán was supported by the Museum of Zoology at the University of Michigan (1951), by the Horace H. Rackham School of Graduate Studies of the University of Michigan (1955), by the Penrose Fund of the American Philosophical Society (1956), by the Bache Fund of the National Academy of Sciences (1958), and by the University of Kansas Endowment Association (1960).

Permits for collecting specimens in México were provided by the Dirección General de Caza through the courtesy of Ing. Juan Lozano Franco and Luis Macías Arellano.

Historical Account

Unlike many parts of southern México and northern Central America, Michoacán received no attention from the collecting expeditions of the European museums in the last century. The earliest known herpetological specimens from Michoacán were obtained by Louis John Xantus, who was appointed U. S. Consul to Colima in 1859. In April, 1863, Xantus collected at Volcán Jorullo in Michoacán; in April and May of the same year he collected along the coast of Michoacán between the Río Cachán and the Río Nexpa. His small collection of 19 extant specimens is in the United States National Museum. Alfredo Dugès, a resident of Guanajuato, México, made early contributions to the knowledge of the herpetofauna of Michoacán. In 1885 he described *Sonora michoacanensis*, and in 1891 he described *Eumeces altamirani*; from what is known of the distribution of these species, he probably had collected in the Tepalcatepec Valley. During their biological survey of México, Edward W. Nelson and Edward A. Goldman spent a limited amount of time in Michoacán in 1892 and again in 1903 and 1904. Most of their collecting was done on the plateau in the north-central part of the state; their collections are in the United States National Museum. While collecting fishes in southern México, Seth E. Meek obtained some amphibians and reptiles from Lago de Pátzcuaro in 1904; these are in the collections of the Chicago Natural History Museum. In 1908 Hans Gadow ventured into the then unexplored "tierra caliente" of the Balsas Valley and collected at Volcán Jorullo and other localities in the valley. Later in the same year he collected at Guayabo, San Salvador, and Arteaga in the Sierra de Coalcomán and at Buena Vista and Co-

fradía in the Tepalcatepec Valley. His collections were deposited in the British Museum (Natural History) and the Naturhistorisches Museum Wien.

The first thirty years of the present century saw little more field work in Michoacán. In the 1930's Edward H. Taylor and Hobart M. Smith collected throughout much of México. At various times they worked in Michoacán, principally along the road from México City to Guadalajara. In 1935 Hobart M. Smith spent a week at Hacienda El Sabino south of Uruapan; he revisted the locality again in 1936 and made a large and important collection of amphibians and reptiles from the upper limits of the arid tropical scrub forest in the Tepalcatepec Valley. Specimens collected by Smith and Taylor were incorporated into the Edward H. Taylor-Hobart M. Smith collection, which subsequently was deposited in part in the Museum of Natural History at the University of Illinois and in part in the Chicago Natural History Museum. In 1939 Hobart M. Smith collected at Pátzcuaro and between Uruapan and Apatzingán; these collections, made while he was a Walter Rathbone Bacon Scholar of the Smithsonian Institution, are deposited in the United States National Museum. In 1940 and 1941 Frederick A. Shannon, who was a member of the Hoogstraal Expeditions under the auspices of the Chicago Natural History Museum, collected on Cerro de Tancítaro and at Apatzingán; an account of the specimens collected there was published by Schmidt and Shannon (1947).

The eruption of Volcán Parícutin in February, 1943, attracted the attention of many biologists, a group of which from the Museum of Zoology at the University of Michigan collected in the Cordillera Volcánica in 1945 and 1947. The amphibians and reptiles were collected and studied by Norman E. Hartweg. In 1950 James A. Peters accompanied Donald D. Brand on a preliminary exploration of the western part of the Sierra de Coalcomán and adjacent Pacific coast of Michoacán; in the same year Peters collected also on the Mexican Plateau and at Volcán Jorullo. His specimens are in the Museum of Zoology at the University of Michigan. Since 1950 many biologists have collected in Michoacán in the course of work on certain groups of animals or in general surveys. In this way Raymond Alcorn, Robert W. Dickerman, James R. Dixon, Floyd L. Downs, Emmet T. Hooper, and Robert R. Miller have contributed to our knowledge of the herpetofauna.

As stated previously, my own field work in Michoacán began in 1951, when I accompanied Donald D. Brand on an exploring

expedition to the southern part of the state. In that year a short time was spent on the Mexican Plateau, principally in the area around Lago de Cuitzeo, and at Volcán Jorullo. In July and August we made our headquarters at Coalcomán. From that town the field party travelled southward to Maruata on the Pacific coast and thence back over the mountains to Coalcomán. Later in that summer we travelled by mule from Coalcomán southeastward to the mouth of the Río Nexpa. In 1955, accompanied by Lee D. Beatty, Carter R. Gilbert, and Fred G. Thompson, I collected in the Tepalcatepec Valley and at Coalcomán. We made a mule trip from Coalcomán to Cerro de Barolosa, where we made the first collections from the pine-fir forests in the Sierra de Coalcomán. Later in the same summer Carter R. Gilbert and I spent a week at Playa Azul on the Pacific coast. In March, April, and May, 1956, my wife and I collected for a short time in the Cordillera Volcánica and on the Mexican Plateau. In early April we moved into the Tepalcatepec Valley, where we collected intensively between Churumuco and Tepalcatepec. In May we collected on the Pacific coast between Boca de Apiza and La Placita. In July and August, 1956, accompanied by Richard E. Etheridge, we returned to Michoacán and again collected on the Mexican Plateau and in the Cordillera Volcánica, before moving into the Tepalcatepec Valley. In an attempt to fill in gaps in the known distributions of many species and to sample the fauna in some previously uncollected areas, I returned to Michoacán in June, 1958. Accompanied by Jerome B. Tulecke and John Wellman, I collected on the Mexican Plateau in the northwestern part of the state, on the southern slopes of the Cordillera Volcánica, and in the Tepalcatepec Valley. Most of our time was spent in the Sierra de Coalcomán, where we collected at Aguililla, Artega, and Dos Aguas. In 1960 two days were spent in Michoacán; a small collection was made in the eastern part of the Cordillera Volcánica. With the exception of the specimens collected in 1960, which are at the Museum of Natural History at the University of Kansas, the specimens that I have collected in Michoacán are in the Museum of Zoology at the University of Michigan.

NATURAL LANDSCAPE

A proper understanding of the geographical distribution of animals in a given region is possible only after a thorough acquaintance with the geography of the region. Likewise, in order to gain a knowledge of the ecological distribution and relationships of the

components of the fauna, it is necessary to study the animals in their natural environments. In order to give the reader a picture of the physical features and the major animal habitats within the state of Michoacán, the following brief description is offered. Each of these facets mentioned below will be elaborated in detail in my final report on the herpetofauna of Michoacán.

Physiography

The state of Michoacán comprises an area of 60,093 square kilometers (Vivó, 1953). Within this area the rugged terrain has a total relief of nearly 4000 meters. There have been several attempts to classify the physiographic provinces of México; the classification used here is a slight modification of the scheme proposed by Tamayo (1949). I have tried to keep the system as simple as possible, but still useful in discussing the distribution of animals living in the region. For general purposes the state of Michoacán can be divided into lowlands and highlands as follows:

Lowlands
- Pacific Coastal Plain
- Balsas-Tepalcatepec Basin

Highlands
- Mexican Plateau
- Cordillera Volcánica
- Sierra de Coalcomán

Although the lowlands in the state are continuous, they are only narrowly connected and thus form two distinct physiographic and biotic areas. The Pacific Coastal Plain in Michoacán extends for a distance of about 200 kilometers (airline) from the Río Coahuayana to the Río Balsas. The coastal plain is broad between the Río Coahuayana and San Juan de Lima, and between Las Peñas and the Río Balsas, where the hills rise some 12 kilometers inland from the sea. Between San Juan de Lima and Las Peñas the mountains extend to the sea; in this region rocky promontories form precipitous cliffs dropping into the sea. Between the promontories are small sandy or rocky beaches.

Lying to the north of the Sierra de Coalcomán and the Sierra del Sur, but south of the Cordillera Volcánica, is a broad structural depression, the Balsas-Tepalcatepec Basin. The western part of this basin, which separates the Sierra de Coalcomán from the Cordillera Volcánica, is the valley of the Río Tepalcatepec, a major tributary of the Río Balsas. The eastern part of the basin is the valley of the Río Balsas. From the point of junction of the two rivers, the Río Balsas flows southward through a narrow gorge,

which separates the Sierra de Coalcomán from the Sierra del Sur, to the Pacific Ocean. In Michoacán the floor of the Balsas-Tepalcatepec Basin varies from 200 to 700 meters above sea level.

The central part of México is a vast table-land, the Mexican Plateau, the southern part of which extends into northern Michoacán. In this region the terrain is rolling and varies from 1500 to 1900 meters above sea level. Many small mountain ranges rise from the plateau and break the continuity of the rolling table-land. Located on the southern part of the Mexican Plateau in Michoacán are several lakes, the largest of which are Lago de Chapala, Lago de Cuitzeo, and Lago de Pátzcuaro.

Bordering the southern edge of the Mexican Plateau is a nearly unbroken chain of volcanos, the Cordillera Volcánica. The highest peaks in Michoacán, Cerro San Andrés (3930 meters) and Cerro de Tancítaro (3870 meters), are in this range. Parts of the Cordillera Volcánica in Michoacán are known by separate names; these are, from west to east: Sierra de los Tarascos, Sierra de Ozumatlán, and Serranía de Ucareo.

Lying between the Tepalcatepec Valley and the Pacific Ocean, and east of the Río Coahuayana and west of the Río Balsas, is an isolated highland mass, the Sierra de Coalcomán. This mountain range rises to elevations of slightly more than 3000 meters. It has a length of about 200 kilometers and a width of about 80 kilometers. Except for a relatively low connection with the Cordillera Volcánica, the Sierra de Coalcomán is isolated from other mountain ranges in southwestern México.

CLIMATE

The climates in Michoacán vary from tropical in the lowlands to cool temperate at high elevations in the Sierra de Coalcomán and Cordillera Volcánica. The highest temperatures are known in the Balsas-Tepalcatepec Basin, where at Churumuco the mean annual temperature is 29.3° C. and the range of monthly means is 3.5° C. (Contreras, 1942). Frosts occur sporadically on the Mexican Plateau, and in the winter snow falls on the highest mountains.

Precipitation varies geographically and seasonally. Most of the rain falls between June and October. In the Balsas-Tepalcatepec Basin rainfall in the rest of the year is negligible. The annual average rainfall at Coahuayana on the Pacific Coastal Plain is 871 mm. (Guzmán-Rivas, 1957:52). In the Balsas-Tepalcatepec Basin rainfall seldom exceeds 800 mm. per year. In the mountains precipitation is heavier and somewhat more evenly distributed throughout the

year, but still definitely cyclic. For example, Uruapan (elevation, 1500 meters) receives an average annual rainfall of 1674 mm. (Contreras, 1942). The prevailing winds are from the Pacific Ocean. The southern (windward) slopes of the Sierra de Coalcomán probably receive more rain than any other part of the state. The Balsas-Tepalcatepec Basin lies in a rain shadow of the Sierra de Coalcomán, and the Mexican Plateau lies in a somewhat less drastic rain shadow of the Cordillera Volcánica; these are the driest regions in the state.

VEGETATION AND ANIMAL HABITATS

For the purposes of this report I have adopted the classification of types of vegetation that seem to me most significant in terms of ecological distribution of reptiles and amphibians in Michoacán. These types are as follows:

TEMPERATE (1000-4000 meters)
- Fir Forest (2400-4000 meters)
- Pine-oak Forest (1000-4000 meters)
- Mesquite-grassland (1500-2100 meters)

TROPICAL (0-1000 meters)
- Arid Tropical Scrub Forest (0-1000 meters)
- Tropical Semi-deciduous Forest (150-600 meters)

The vegetation of the Pacific Coastal Plain and the Balsas-Tepalcatepec Basin consists of arid tropical scrub forest, composed of deciduous trees, which in many places are stunted and widely spaced. In the dry season there is little cover provided by this forest. In the rainy season there is a sparse growth of grasses and some shade provided by the small leaves of the thorny trees.

In Michoacán the rainfall is heaviest on the southern slopes of the Sierra de Coalcomán and somewhat less so on the southwestern slopes of the Cordillera Volcánica. At these relatively low elevations (150 to 600 meters) there is tropical semi-deciduous forest, characterized by relatively dense shade throughout the year and by a leaf mulch on the ground. This type of forest forms the gallery forest along the larger streams in the Balsas-Tepalcatepec Basin and on the Pacific Coastal Plain.

Rainfall also is heavy on the high mountain ridges, where temperatures are low. On these ridges, fir forest, often mixed with pine and oaks, is found. This habitat is characterized by a cool, moist climate, many rotting logs, and a moist ground cover of leaves and needles.

Most of the mountains are covered with pine-oak forest, which in most places is decidedly subhumid, but where this forest occurs on the windward sides of high ridges, it sometimes is noticeably

humid. In this forest the important animal habitats include the needle- and leaf-litter, and in some areas, bromeliads.

The rolling terrain of the Mexican Plateau supports cacti, small leguminous trees, and grasses. Like the arid tropical scrub forest, this type of vegetation, the Mesquite-grassland association, is deciduous and thus provides little shelter in the dry season. Unlike the areas in which arid tropical scrub forest is developed, the Mesquite-grassland is found in areas having warm days and cool nights.

GEOGRAPHY OF THE HERPETOFAUNA

Although the main part of my final report on the herpetofauna of Michoacán will deal with the geographical and ecological patterns of distribution of the herpetofauna, a brief summary of the faunal assemblages is presented here.

In Michoacán there are two major faunal assemblages, one in the lowlands, and one in the highlands. A large number of the species inhabiting the lowlands are wide-ranging species, such as *Bufo marinus, Iguana iguana,* and *Boa constrictor.* Sixty-three species are known to occur on the Pacific Coastal Plain; 41 of these, together with 36 others occur in the Balsas-Tepalcatepec Basin, a physiographic region to which several species of reptiles are endemic; for example, *Enyaliosaurus clarki, Urosaurus gadowi, Cnemidophorus calidipes,* and *Eumeces altamirani.*

Generally speaking, the members of the highland faunal assemblage have more restricted geographic ranges. The major exceptions are those species that are widely distributed on the Mexican Plateau, such as: *Bufo compactilis, Sceloporus torquatus,* and *Salvadora bairdi.* In the montane habitats of the Cordillera Volcánica, 45 species of amphibians and reptiles are known; 34 species have been found in the Sierra de Coalcomán. Fourteen species are known to occur in both ranges. Several species are known only from the Cordillera Volcánica and adjacent highlands, and three species are endemic to the Sierra de Coalcomán.

ANNOTATED LIST OF SPECIES

In the following pages the 176 species and subspecies of amphibians and reptiles known to occur in the state of Michoacán are discussed in relation to their variation, life histories, ecology, and distribution in the state. Data have been gathered from 9676 specimens. I have not prolonged the accounts of species with information that has been presented elsewhere. Consequently, the length and completeness of the accounts are variable. I have given only the information that I consider a worthwhile contribution to our knowledge of the particular species.

The synonymies given at the beginning of each account include the first use of the trivial name by the original author, the first usage of the combination that I am using, and, if the circumstances make it necessary, additional names or combinations that have been proposed since the publication of the checklists of Mexican amphibians and reptiles by Smith and Taylor (1945, 1948, and 1950b). References cited only in the synonymies are not listed in the Literature Cited. Preceding the discussion of each species is an alphabetical list of the localities in Michoacán from which specimens have been examined. The listing of a locality means that one or more specimens, as indicated, has been examined from that locality. Only for those specimens especially mentioned in the text are catalogue numbers given. Abbreviations for the various museums and scientific collections are, as follows:

AMNH	American Museum of Natural History
ANSP	Academy of Natural Sciences of Philadelphia
BMNH	British Museum (Natural History)
CNHM	Chicago Natural History Museum
EHT-HMS	Edward H. Taylor-Hobart M. Smith collection
JRD	James R. Dixon collection, College Station, Texas
KU	University of Kansas Museum of Natural History
MCZ	Museum of Comparative Zoology
MVZ	Museum of Vertebrate Zoology
NMW	Naturhistorisches Museum Wien
SU	Stanford University Museum of Natural History
TCWC	Texas Cooperative Wildlife Collection
UIMNH	University of Illinois Museum of Natural History
UMMZ	University of Michigan Museum of Zoology
USNM	United States National Museum
UTNHC	University of Texas Natural History Collection

Throughout the accounts of the species all measurements are given in millimeters; if the range of variation is given, the mean follows in parentheses.

AMPHIBIA

Caudata

Ambystoma amblycephalum Taylor

Ambystoma amblycephala Taylor, Univ. Kansas Sci. Bull., 26: 420, November 27, 1940.—Fifteen kilometers west of Morelia, Michoacán, México.

Fifteen km. W of Morelia (19); 11 km. SSE of Opopeo (12); 8 km. S of Pátzcuaro; 24 km. S of Pátzcuaro (2); Quiroga (20); Tacícuaro (167).

Taylor and Smith (1945:530) presented data on 137 specimens collected at Tacícuaro on October 1, 1939; these are all larvae and metamorphosing individuals. Aside from these, the largest larva examined (UMMZ 104962 from 15 km. W of Morelia) has a snout-vent length of 70.0 mm. and a tail length of 53.5 mm. The larvae are pale pinkish tan above and somewhat paler below; there is a lateral row of cream colored spots. The tail-fin, which is deepest at mid-length, extends to the back of the head and is flecked with brown. In small larvae the outer edge of the tail-fin is dark brown. The eyes are large. Two small metamorphosed specimens (UMMZ 98967) from 24 kilometers south of Pátzcuaro are tenta-

tively referred to this species. These specimens have body lengths of 49.0 and 45.0 mm. and tail lengths of 36.0 and 31.5 mm., respectively. They have 17-17 and 16-15 vomerine teeth arranged in a broad arch behind the choanae, 10 costal grooves, and 7 intercostal spaces between adpressed toes. The dorsal color is uniform brown; that of the venter is a dusty cream.

Larvae were collected from shallow ponds near Quiroga and 15 kilometers west of Morelia; metamorphosed individuals were taken from beneath logs in pine and fir forests at elevations from 2300 to 2800 meters.

Ambystoma dumerili dumerili (Dugès)

Siredon Dumerili Dugès, La Naturaleza, 1:241, 1870—Lago de Pátzcuaro, Michoacán, México.

Bathysiredon dumerilii, Dunn, Notulae Naturae, 36:1, November 9, 1939.

Bathysiredon dumerilii dumerilii, Maldonado-Koerdell, Mem. y Rev. Acad. Nac. Cien., 56:199, 1948.

Ambystoma (Bathysiredon) dumerili, Tihen, Bull. Florida State Mus., 3:3, June 20, 1958.

Lago de Pátzcuaro (22); ? Morelia.

For many years this unusual salamander was known from only a few specimens mostly collected in the last century; Smith and Taylor (1948:7) stated: "It is presumed that this species is extinct owing to the introduction of exotic game and food fishes." In 1951 and in 1955 I had been told that *axolotls* were sold in the market at Pátzcuaro; nevertheless, none was found on my visits there. In 1956 Charles M. Bogert obtained several large specimens at the market in Pátzcuaro. These establish the continued existence of the salamander in Lago de Pátzcuaro. On January 27, 1955, R. W. Dickerman procured a specimen (KU 41573) in the market at Morelia. Since fish are brought to Morelia from Lago de Pátzcuaro, the specimen probably was from that lake. Nevertheless, the species may occur in other permanent bodies of water in Michoacán. Maldonado-Koerdell (1948) described *Bathysiredon dumerili queretarensis* from San Juan del Río, Queretaro. This locality is about 200 airline kilometers northeast of Lago de Pátzcuaro and is in the Río Moctezuma drainage.

Ambystoma ordinarium Taylor

Ambystoma ordinaria Taylor, Univ. Kansas Sci. Bull., 26:422, November 27, 1940.—Four miles west of El Mirador, near Puerto Hondo, Michoacán, México.

Axolotl (56); Cerro San Andrés; 22 km. W of Mil Cumbres; 46 km. E of Morelia (34); 8 km. SE of Opopeo (5); Puerto de Garnica (8); Puerto Hondo (41); San Gregorio (16); San José de la Cumbre (20).

Of 16 specimens (KU 51520-35) collected on June 18, 1955, near San Gregorio, 15 are adult females with swollen cloacae and minute ovarian eggs. Possibly these specimens had just recently deposited their mature eggs. In preservative the specimens are black above and dull creamy gray below. Measurements for the 15 females are: snout-vent length, 80.0-102.0 (92.5); tail length, 69.0-93.0 (84.2); head width, 15.8-20.5 (17.7); head length, 22.8-26.6 (24.4). A larval specimen with small gills has a snout-vent length of 72 mm. and a tail length of 62 mm. Three specimens have 12 costal grooves; the other have 11.

Of 20 specimens from San José de la Cumbre (UMMZ 112857 and 115143), 14 are neotenic adults; the others are larvae. In life the salamanders were blackish to olive-brown above with scattered cream-colored dots on the dorsum and flanks but in preservative are dull grayish black with indistinct pale spots and dark reticulations. The belly is pale gray with indistinct dark spots. Eleven females and three males have the following measurements, respectively: snout-vent length, 76.0-90.0 (80.7), 64.0-84.0 (74.3); tail length, 70.0-81.0 (75.0), 58.0-71.0 (66.7); head width, 19.5-23.5 (20.7), 17.5-20.5 (19.3); head length, 22.0-25.0 (23.0), 20.0-22.5 (21.5). The smallest larva has a snout-vent length of 43.0 mm. and a tail length of 38.0 mm. Two individuals have 12 costal grooves; the others have 11. All of the females contained eggs, the largest of which were 1.5 mm. in diameter. The stomachs of most of the specimens were distended with oligochaets, aquatic insect larvae, and small aquatic beetles.

A series of 34 larvae (JRD 5904-37) from 46 kilometers east of Morelia are tentatively referred to this species. These specimens are olive-brown above with cream-colored spots on the flanks; the dorsal tail-fin does not extend onto the body.

This species has been found only at elevations in excess of 2400 meters in pine and fir forests. At Rancho Axolotl James A. Peters collected larvae and neotenic individuals in a rocky stream and adults from beneath rocks and logs in the forest near the stream. Neotenic individuals and larvae were found in a clear stream in pine-fir forest at an elevation of 2700 meters near San José de la Cumbre; specimens were collected there in July, 1955, and again in July, 1956. The site was visited in April, 1956, at which time the stream consisted of only a few puddles; no salamanders were found.

Ambystoma tigrinum velasci Dugès

Ambystoma velasci Dugès, La Naturaleza, ser. 2, 1:142, 1888.—Laguna Santa Isabel, near Guadalupe Hidalgo, Distrito Federal, México.

Ambystoma tigrinum velasci, Dunn, Copeia, no. 3:157, November 14, 1940.

Pátzcuaro (5); Tacícuaro (9).

Definite specific assignment of these specimens, all larvae, cannot be made at this time. They have shovel-shaped heads and laterally compressed bodies with the dorsal tail-fin extending anteriorly to the back of the head. The eyes are small. The body is pale tan with dark mottling on the tail and flanks. The average snout-vent length for nine specimens from Tacícuaro is 61.0 mm.

The larvae from Tacícuaro (UMMZ 89255) were collected by Dyfrig Forbes in October, 1939; those from Pátzcuaro, presumably Lago de Pátzcuaro (BMNH 1914.1.28-247-8 and CNHM 948), were collected by Hans Gadow and Seth Meek in 1908.

Pseudoeurycea belli (Gray)

Spelerpes belli Gray, Catalogue Batrachia Gradientia British Museum, p. 46, 1850.—México. Type locality restricted to 2 miles east of Río Frío, Puebla, México, by Smith and Taylor (1950a:341).

Pseudoeurycea bellii, Taylor, Univ. Kansas Sci. Bull., 30:209, June 12, 1944.

Axolotl (2); Carapan; Cerro Tancítaro (84); Macho de Agua; 22 km. W of Mil Cumbres; Opopeo; Pátzcuaro (8); Puerto Hondo (2); San José de la Cumbre; San Juan de Parangaricutiro (42); Uruapan (5); Zacapu (4).

This salamander seems to reach its greatest abundance in Michoacán in the Sierra de los Tarascos between Pátzcuaro and Tancítaro, where it is found at elevations from 1500 to 2900 meters. It is found less commonly in the eastern part of the Cordillera Volcánica in Michoacán, where it sometimes occurs in association with *Pseudoeurycea robertsi.*

On June 22 and 23, 1955, four clutches of eggs of this species were found beneath adobe bricks and rocks on the volcanic ash that has buried the village of San Juan de Parangaricutiro. The eggs were unstalked and separate, but adherent in clumps of three or four (Pl. 2, Fig. 1). The outer membranes were covered with fine particles of ash. The ash beneath the stones where the eggs were found was only slightly moist; one clump of eggs was partially desiccated. Three complete clutches have 20, 23, and 34 eggs; one clutch of 15 eggs was being eaten by beetles (Tenebrionidae: *Eleodes* sp.). The eggs vary in size from 4.6 to 6.5 mm. and average 5.3 mm. in diameter. They are unpigmented. Surrounding the embryo is a vitelline membrane, an inner, and an outer envelope (Fig. 1). In an

average-sized egg having an embryo 4 mm. in length, the diameter of the outer membrane is 5.3 mm., the inner membrane 5.0 mm., and the vitelline membrane 4.6 mm. All of the eggs contained embryos in which the limb buds were developed; in about half of these the eyes were distinctly visible.

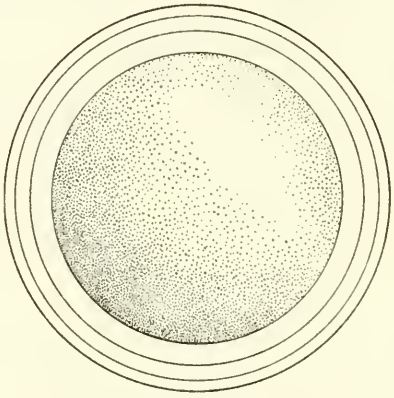


Fig. 1. Diagram of an egg of *Pseudoeurycea belli* from San Juan de Parangaricutiro, Michoacán. × 10.

The first heavy rain of the season occurred on the night of June 22, 1955. Thus, at least sometimes, *Psuedoeurycea belli* lays its eggs before the onset of the rainy season. A female having a snout-vent length of 110 mm., collected on June 22, 1955, contained 36 ovarian eggs having diameters from 3.0 to 3.5 mm. The fact that small juveniles were collected on the same date indicates that this salamander lays eggs over a period of several weeks in late spring and early summer.

The smallest juvenile examined has a snout-vent length of 17.0 mm. and a tail length of 7.5 mm. Twelve juveniles from the vicinity of San Juan de Parangaricutiro have an average snout-vent length of 19.4 mm. and an average tail length of 9.7 mm. In juveniles the adpressed limbs either touch or overlap by one intercostal space; in adults there are two or three intercostal spaces between adpressed toes. Therefore the greatest number of intercostal spaces between adpressed limbs is found in the largest specimens. A similar relationship between adpressed limbs (= length of limbs) and snout-vent length was shown for *Plethodon richmondi* by Duellman (1954a). The number of vomerine teeth is variable; the number of teeth seems to be closely correlated with the size of the salamander (Fig. 2). A similar correlation between the number of

maxillary teeth and body length was reported for *Chiropterotriton multidentatus* by Rabb (1958). In 12 juvenile *Pseudoeurycea belli* there are 6-13 (8.8) vomerine teeth, and in 11 adults having snout-vent lengths greater than 90 mm. there are 39-49 (44.0) vomerine

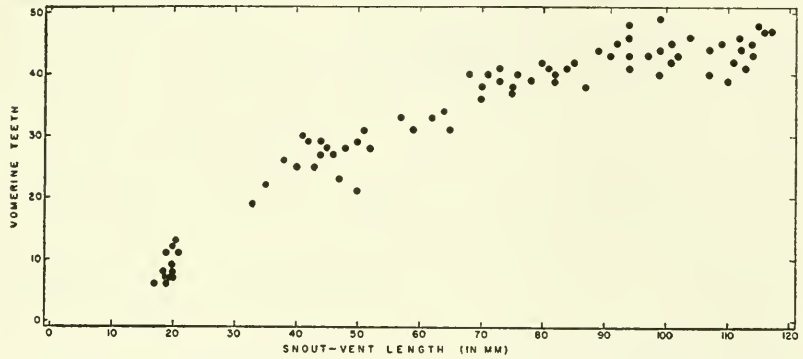


FIG. 2. Correlation between the number of vomerine teeth and snout-vent length in 79 *Pseudoeurycea belli* from Michoacán.

teeth. The coloration of the juveniles resembles that of the adults (Pl. 1).

The differences between this species and *Pseudoeurycea gigantea* are minor. Taylor (1939a) distinguished *gigantea* from *belli* by the larger size, fewer intercostal spaces between adpressed limbs, more vomerine teeth, and absence of occipital spots in *gigantea.* Taylor and Smith (1945) stated that in life the spots in *gigantea* are orange instead of red as in *belli.* Five specimens of *Pseudoeurycea belli* from Michoacán, including one juvenile, lack occipital spots. In the 34 living individuals that I have seen from Michoacán the spots varied from deep red to orange. Therefore, of the characters listed by Taylor (*op. cit.*) to diagnose *Pseudoeurycea gigantea,* only the over-all larger size and smaller number of intercostal spaces between adpressed limbs (= relatively longer limbs) are useful in separating *Pseudoeurycea belli* and *gigantea.*

Pseudoeurycea robertsi (Taylor)

Oedipus robertsi Taylor, Univ. Kansas Sci. Bull., 25:287, July 10, 1939.—Nevado de Toluca, México.

Pseudoeurycea robertsi Taylor, Univ. Kansas Sci. Bull., 30:209, June 12, 1944.

Atzimba (3); Macho de Agua (9); Puerto Lengua de Vaca (14).

Previously this species has been recorded only from the type locality. In July, 1956, individuals referable to this species were found at two sites in pine-fir forest immediately to the east of Macho de Agua and in pine-oak-fir forest at Atzimba. On August 20, 1958,

a series was collected in pine-fir forest at Puerto Lengua de Vaca. These localities are between 2900 and 3000 meters in the Cordillera Volcánica in eastern Michoacán.

In life the coloration of these salamanders was highly variable. The belly and undersurfaces of the tail and hind limbs were pale gray, with or without silvery white flecks; the chin was a cream-color and flecked with silvery white in some specimens. The middorsal area was brown, orange-brown, or dull grayish yellow. The flanks and lateral surfaces of the tail were black with yellowish flecks or streaks on the flanks and yellowish or orange-brown flecks on the tail. The iris was golden brown. Measurements of eight males and two females are, respectively: snout-vent length, 42.5-56.0 (49.5), 54.0-60.0 (57.0); tail length, 42.0-56.0 (48.1), 52.0-55.0 (53.5). The smallest juvenile has a snout-vent length of 28.0 mm. and a tail length of 23.0 mm. Of the 26 available specimens, six have 12 costal grooves, and the others have 11.

In comparison with 36 topotypes, the specimens from Michoacán have a less striking dorsal color pattern; none has a well-defined dorsal reddish brown area or bold reddish mottling on the tail. Furthermore, the specimens from Michoacán have paler venters than do topotypic specimens.

Salientia

Rhinophrynus dorsalis Duméril and Bibron

Rhinophrynus dorsalis Duméril and Bibron, Erpétologie générale, vol. 8:758, 1841.—Veracruz, Veracruz, México.

Mouth of the Río Balsas (10).

These specimens (BMNH 1914.1.28.181-90) were collected by Gadow in 1908 and reported by him (1930:72): "Whilst this very sluggish termite-eating toad is common enough in the sweltering hot country of the state of Vera Cruz, up to an elevation of 1500 feet, it was unknown on the west side of the Isthmus until I found it in great numbers near the mouth of the Balsas River, in and near freshwater pools, where it attracted attention by its loud peculiar voice during the pairing season in the month of July." Subsequently, Peters (1954:3) verified the identification of these specimens. Although torrential rains fell during the week in July, 1955, that I spent at Playa Azul near the mouth of the Río Balsas, the distinctive voice of *Rhinophrynus* was not heard. Elsewhere on the Pacific coast of México adult *Rhinophrynus* have been reported only from Tehuantepec and a few localities on the coastal lowlands of Chiapas. Taylor (1942b:37) found on the coast of Guerrero a tadpole that was re-

ferred to the genus *Rhinophrynus* by Orton (1943). In the summer of 1960 adults of *Rhinophrynus* were collected near Acapulco, Guerrero (Fouquette, *in litt.*). These recent collections verify the existence of the species along the Pacific lowlands of México at least as far north as Michoacán.

Scaphiopus hammondi multiplicatus Cope

Scaphiopus multiplicatus Cope, Proc. Acad. Nat. Sci. Philadelphia, 15:52, June 8, 1863.—Valley of México.

Scaphiopus hammondi multiplicatus, Kellogg, Bull. U. S. Natl. Mus., 160:22, March 31, 1932.

Angahuan (5); Cuitzeo (4); Cuseño Station (2); Jiquilpan (9); Morelia (7); Pátzcuaro (3); Quiroga; Tarécuaro; Uruapan (24); Zacapu.

This small toad has been found at elevations between 1500 and 2500 meters on the Mexican Plateau and associated mountain ranges; it occurs in mesquite-grassland and in pine forests. Calling males and females laden with eggs have been collected in the rainy season in the months of July and August. The call is a medium-pitched snore. In living individuals the dorsal ground color varies from pale brown to gray with dark brown or olive-brown markings. In many individuals the tips of the small dorsal pustules are red.

Bufo coccifer Cope

Bufo coccifer Cope, Proc. Acad. Nat. Sci. Philadelphia, 18:130, 1866.—Arriba, Costa Rica.

Apatzingán (27); Lombardia; Nueva Italia (5).

In life the dorsal color pattern consists of a yellowish tan ground color with dark brown spots; the middorsal stripe is deep yellow or cream color. The venter is a dusty cream color, and the iris is pale gold. Males have dark brown horny nuptial tuberosities on the thumb. The following measurements are of 21 males and four females, respectively: snout-vent length, 43.5-51.7 (48.1), 55.6-62.6 (59.1); tibia length, 16.6-18.8 (17.6), 18.8-20.3 (19.3); head width, 16.7-19.7 (18.4), 20.6-22.2 (21.4); head length, 13.8-16.6 (14.8), 16.5-18.2 (17.3).

The specimens from the Tepalcatepec Valley differ slightly from specimens from southeastern México and Central America. Those from Michoacán have low and narrow cranial crests; in about one-half of the specimens the occipital crest exists only as a row of tubercles, and in some the postorbital and suborbital crests are barely discernible. Specimens from the southern part of the range, Costa Rica and Nicaragua, have much higher and thicker cranial crests; in these the occipital crest is well defined and extends pos-

teriorly to a point back of the anterior edge of the parotid gland; the postorbital and suborbital crests are well marked. Of 48 specimens from Esquipulas, Guatemala, all have high crests, but these are not so well developed as in ten specimens from Matagalpa, Nicaragua, and three from various localities in Costa Rica. Six specimens from Tehuantepec, Oaxaca, have cranial crests that are lower than those in specimens from Guatemala. In three of the specimens from Tehuantepec the occipital crests are reduced to a series of tubercles. Of six specimens from Agua del Obispo, Guerrero, four have poorly developed occipital crests. These observations suggest the presence of a cline in the development of the cranial crests; specimens have higher crests in the southern part of the range than in the northern part.

In México *Bufo coccifer* has been collected only in semi-xeric habitats, but to the south, from Guatemala to Costa Rica, it has been found in more upland and humid habitats. Southern specimens are darker than those from the north, a possible correlation with the differences in habitat.

These toads probably range throughout the Tepalcatepec Valley, but they are unknown from the coast of Michoacán. Breeding choruses were found after heavy rains on June 24, 1955, and on August 2, 1956. The first was in a muddy ditch; the second was in a flooded grassy field. The call is a high-pitched, but not loud, "whirrr." Males were calling from the edge of the water or from clumps of grass in the water. Clasping pairs were in the water; amplexus is axillary.

Bufo compactilis compactilis Wiegmann

Bufo compactilis Wiegmann, Isis von Oken, 26:661, 1833.—México. Type locality restricted to Xochimilco, Distrito Federal, México, by Smith and Taylor (1950a:330).

Bufo compactilis compactilis, Smith, Herpetologica, 4:7, September 17, 1947.

Cuitzeo (2); Emiliano Zapata (20); Jiquilpan (5); La Palma (5); Morelia; Tupátaro.

The southwestern terminus of the range of this species is on the Mexican Plateau in Michoacán. All specimens from the state have spotted venters. In living toads the dorsal ground color was gray or grayish tan with olive green spots. The vocal sac was brownish gray; the iris was a bright golden color.

On June 11, 1958, many individuals were calling from shallow water in a flooded field at Emiliano Zapata. The call is a slow trill, in which the individual notes are discernible.

Bufo marinus (Linnaeus)

Rana marina Linnaeus, Systema naturae, ed. 10, 1:211, 1758.—America.

Bufo horribilis Wiegmann, Isis von Oken, 26:654, 1833.—Misantla and Veracruz, Veracruz, México. Taylor and Smith, Proc. U. S. Natl. Mus., 95: 551, January 30, 1945.

Bufo angustipes Taylor and Smith, Proc. U. S. Natl. Mus., 95:553, January 30, 1945.—La Esperanza, Chiapas, México.

Aguililla; Apatzingán (3); Barranca de Bejuco; Capirio; Charapendo; Chichihuas; Coahuayana (2); Coalcomán (7); Cofradía (2); 25 km. S of Cuatro Caminos; El Sabino (10); Huahua, La Playa (13); Ojos de Agua de San Telmo; Ostula; Playa Azul (2); Pómaro (2).

This large toad is characteristically found in areas supporting tropical scrub forest to elevations of about 1000 meters. The species is much more abundant than the numbers listed above suggest. In the dry season individuals have been observed in patios, along streams, and by irrigation ditches. In the rainy season the loud, rattling call of the males is heard at night throughout the Tepalcatepec Valley and the coastal lowlands.

Taylor and Smith (1945:552) revived Wiegmann's *Bufo horribilis* for the large toads of México that are here referred to *B. marinus*. Their action was based upon the supposition that the "species *marinus*" is composite. Although probably true, this supposition has yet to be proved. Until the large, and apparently related, species of *Bufo* inhabiting tropical America have been studied systematically as a unit, the recognition of segments of the population as either species or subspecies is meaningless. Taylor and Smith (*op. cit.*:553) based the description of a new species, *Bufo angustipes*, on one rather emaciated, formalin-hardened female from La Esperanza, Chiapas. The type (USNM 116513), when compared with numerous specimens of *Bufo marinus* from throughout the range of the species in México and northern Central America, displays no combination of characters to set it off from the others. Therefore, I suggest that *Bufo horribilis* Wiegmann and *Bufo angustipes* Taylor and Smith be placed in the synonymy of *Bufo marinus* (Linnaeus) until future systematic study of the genus and this species in particular establishes the existence of recognizable taxa.

Bufo marmoreus Wiegmann

Bufo marmoreus Wiegmann, Isis von Oken, 26:66, 1833.—Veracruz, Veracruz, México.

Barranca de Bejuco; Coahuayana (11); El Diezmo (2); La Placita (9); La Orilla (12); Motín del Oro; Ostula (9); Playa Azul (5); Pómaro (15); Salitre de Estopilas; San Pedro Naranjestila.

In Michoacán this species is confined to elevations of less than 1000 meters on the coast and foothills of the Sierra de Coalcomán.

In this region in the months of June and July, breeding congregations have been found in temporary pools and along streams.

Smith and Taylor (1948:39), in their key to the Mexican species of *Bufo,* placed emphasis on the nature of the supraorbital and postorbital crests (whether they form a curve or a sharp angle) in distinguishing *Bufo marmoreus* from *Bufo perplexus.* In the original description of *perplexus,* Taylor (1943a:347) characterized the species as follows: supraorbital and postorbital crests forming a sharp angle, instead of a curve as in *marmoreus;* supratympanic crest smaller than in *marmoreus;* diagonal lateral stripe lacking in females; concentration of dorsal tubercles as found in *marmoreus* lacking in males. The discovery of specimens in which the crests form a curve and others in which the crests form an angle in both the Tepalcatepec Valley and in the coastal lowlands prompted an investigation of these characters and others throughout the ranges of the species. An examination of 410 specimens has resulted in the following conclusions.

Table 1.—Variation in the Shape of the Supraorbital and Postorbital Cranial Crests in Bufo marmoreus and B. perplexus.

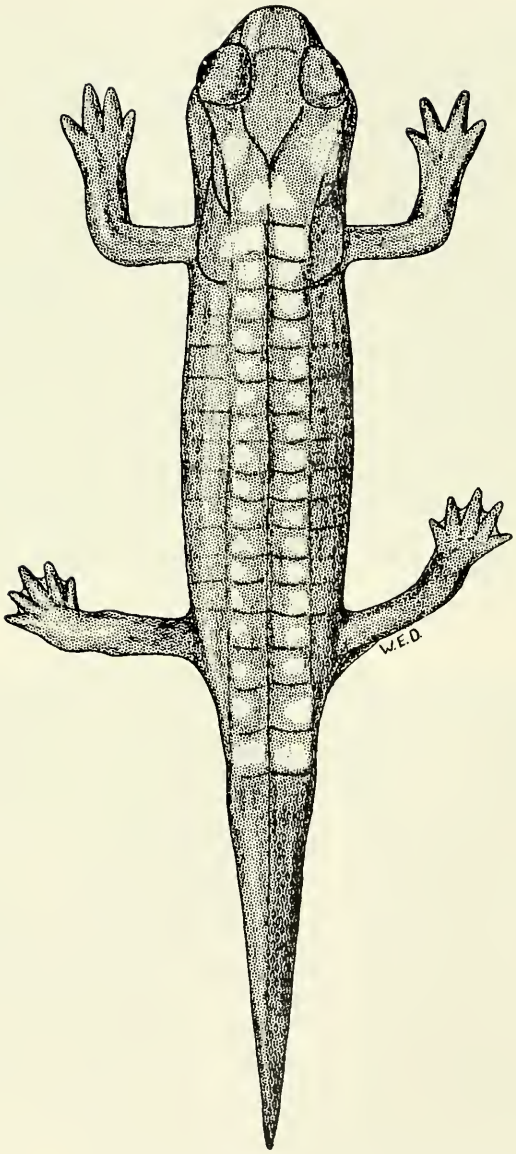
Locality	N	Curved	Intermediate	Angular
Tepalcatepec Valley	50	10 (20.0%)	17 (34.0%)	23 (46.0%)
Morelos	12	2 (16.6%)	5 (41.7%)	5 (41.7%)
Izucar, Puebla	4	2 (50.0%)	0 (0.0%)	2 (50.0%)
Southern Sinaloa	1	1 (100.0%)	0 (0.0%)	0 (0.0%)
Puerto Vallarta, Jalisco	2	2 (100.0%)	0 (0.0%)	0 (0.0%)
Colima	45	25 (55.0%)	18 (40.0%)	2 (5.0%)
Coast of Michoacán	55	35 (63.6%)	17 (30.9%)	3 (5.5%)
Acapulco, Guerrero	7	7 (100.0%)	0 (0.0%)	0 (0.0%)
Chilpancingo, Guerrero	10	1 (10.0%)	4 (40.0%)	5 (50.0%)
Pochutla, Oaxaca	13	6 (46.2%)	6 (46.2%)	1 (7.6%)
Tehuantepec, Oaxaca	177	81 (45.8%)	67 (37.8%)	29 (16.4%)
Tonolá, Chiapas	1	0 (0.0%)	0 (0.0%)	1 (100.0%)
Veracruz	33	26 (78.8%)	6 (18.2%)	1 (3.0%)
Total	410	198 (48.3%)	140 (34.2%)	72 (17.5%)

1. Although the highest percentage of individuals having the supraorbital and postorbital crests forming a sharp angle is from localities in the Balsas-Tepalcatepec Basin, numerous individuals from throughout the range of *marmoreus* have the crests forming an angle (Table 1).
2. In all samples of ten or more specimens, some toads have the supraorbital and postorbital crests forming a sharp angle, some have the crests forming a curve, and some have an intermediate condition.
3. The relative size of the supratympanic crest is highly variable in all samples examined.

FIG. 3. Adult male of *Bufo perplexus* from Apatzingán, Michoacán. × 1.5.

FIG. 4. Adult male of *Bufo marmorcus* from Pómaro, Michoacán. × 1.5.

PLATE 1



Hatchling of *Pseudoeurycea belli* from San Juan de Parangaricutiro, Michoacán. × 8.

PLATE 4

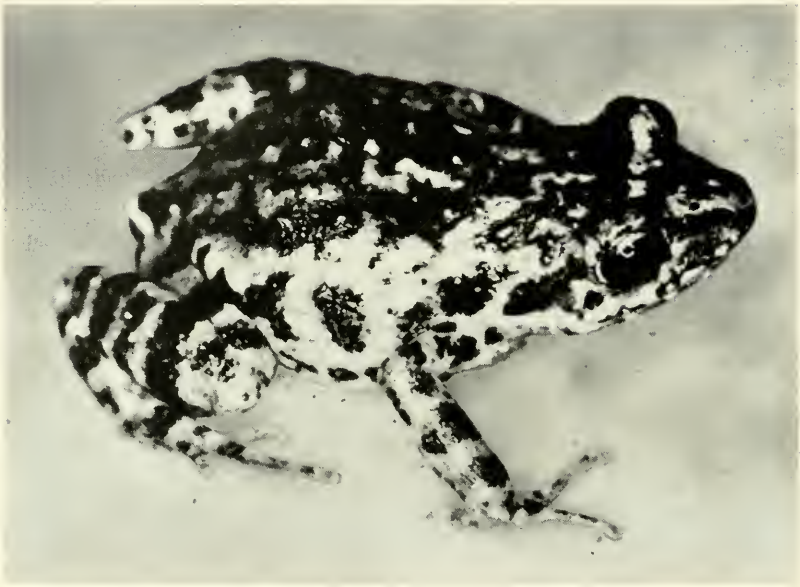


FIG. 1. Adult male of *Tomodactylus nitidus nitidus* from Tuxpan, Michoacán. × 4.

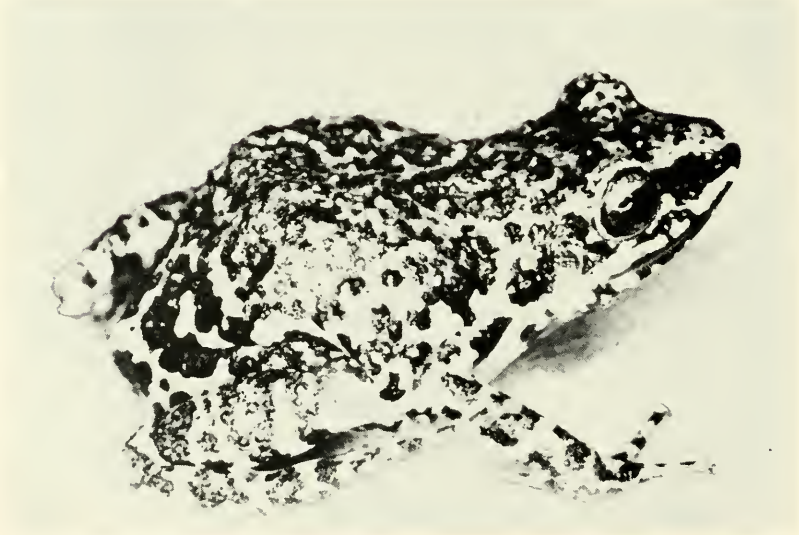


FIG. 2. Adult male of *Tomodactylus nitidus orarius* from Tecolapa, Colima. × 4.

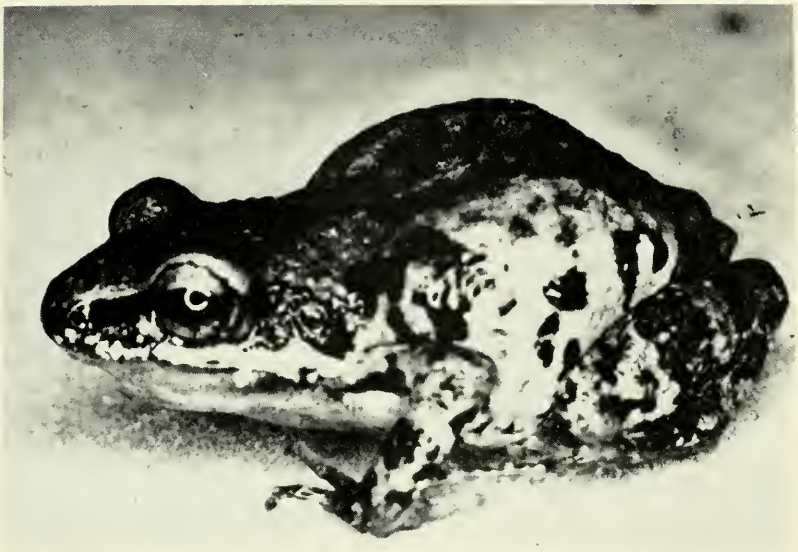


FIG. 1. Adult male of *Tomodactylus nitidus petersi* from Apatzingán, Michoacán. × 4.

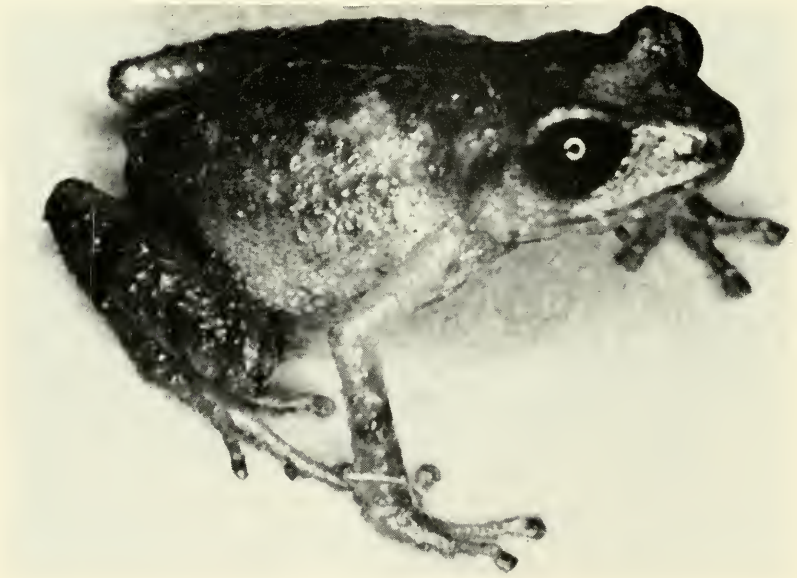


FIG. 2. Adult male of *Tomodactylus rufescens* from Dos Aguas, Michoacán. × 4.

PLATE 6

FIG. 1. Adult male of *Hypopachus caprimimus* from Tuxpan, Michoacán. × 2½.

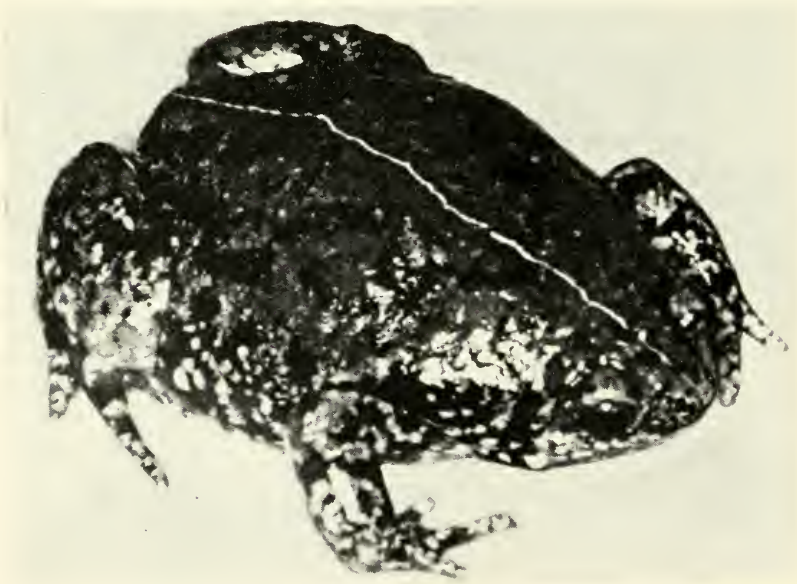


FIG. 2. Adult male of *Hypopachus oxyrrhinus ovis* from Tangamandapio, Michoacán. × 3.

4. A distinct, pale-colored, diagonal lateral stripe is found in females only from localities outside of the Balsas-Tepalcatepec Basin; females from the basin have a spotted dorsum.
5. Males from the Balsas-Tepalcatepec Basin usually have a broad middorsal line that is yellow or pale tan; those from outside the basin have either a narrow middorsal line or none.
6. Males from the Balsas-Tepalcatepec Basin have low, scattered dorsal tubercles (Fig. 3); males from outside the basin have a concentration of tubercles in a broad band on the back (Fig. 4).

Therefore the nature of the cranial crests is of little value in separating two populations, but the color pattern of the females and the nature of the dorsal tubercles of the males do show distinct differences. Furthermore, certain differences in size and proportion are evident; *Bufo marmoreus* is a slightly larger toad and has a relatively longer tibia and longer head than *perplexus* (Table 2).

TABLE 2.—COMPARISON OF CERTAIN MEASUREMENTS AND PROPORTIONS IN BUFO MARMOREUS AND B. PERPLEXUS. (MEANS ARE GIVEN IN PARENTHESES BELOW THE RANGES.)

SPECIES	Sex	N	Snout-vent length	Tibia length / Snout-vent length	Head length / Snout-vent length
B. marmoreus	♂	15	61.5–72.5 (65.2)	35.9–41.6 (39.0)	28.3–33.3 (31.6)
B. perplexus	♂	20	50.0–59.0 (54.9)	33.7–38.1 (36.4)	26.4–31.1 (29.5)
B. marmoreus	♀	7	68.0–76.0 (70.7)	33.0–36.8 (34.7)	26.8–32.6 (29.6)
B. perplexus	♀	6	64.1–69.8 (66.8)	32.4–36.9 (35.5)	25.1–29.0 (27.5)

Taylor (1943a:347) described *Bufo perplexus* from Mexcala on the Río Balsas in Guerrero. Among the many paratypes are specimens from Tonolá, Chiapas, and Tehuantepec, Oaxaca. These apparently were referred to *perplexus* solely on the nature of the cranial crests. All of the specimens examined during the course of the present study from the lowlands of Veracruz and from the Pacific lowlands from Sinaloa southward to Chiapas are referable to *Bufo marmoreus;* those from the Balsas-Tepalcatepec Basin are referable to *Bufo perplexus,* as defined above. Ten specimens from Chilpancingo, Guerrero (UNMZ 115352), do not readily fit either species. Perhaps there is gene exchange between the inland and

coastal populations through the relatively low pass at Chilpancingo, at the mouth of the Río Balsas, and near the convergent headwaters of the Río Coahuayana and Río Tepalcatepec in southern Jalisco. If this can be demonstrated, then *Bufo perplexus* would have to be considered as a subspecies of *Bufo marmoreus*, instead of an allopatric species.

Bufo perplexus Taylor

Bufo perplexus Taylor, Univ. Kansas Sci. Bull., 29:347, October 15, 1943.—Balsas River near Mexcala, Guerrero, México.

Aguililla (2); Apatzingán (42); Buena Vista (5); Capirio (3); La Playa (25); Lombardia (6); Nueva Italia (9); Río Cancita, 14 km. E of Apatzingán; Río Tepalcatepec, 27 km. S of Apatzingán; San Salvador (4); Tzitzio; Volcán Jorullo.

Bufo occidentalis Camerano

Bufo occidentalis Camerano, Atti R. Accad. Sci. Torino, 14:887, December 31, 1878.—México. Type locality restricted to Guanajuato, Guanajuato, México, by Smith and Taylor (1950a:330). Firschein, Copeia, no. 3:220, September 15, 1950.

Bufo simus, Smith and Taylor, Bull. U. S. Natl. Mus., 194:42, 1948.

Barranca Seca (32); Cerro de Barolosa (4); Cerro Tancítaro, 3 km. E of Apo (2); Cerro Tancítaro, 19 km. E. of Apo (10); Charapendo; Coalcomán (7); Dos Aguas (4); Jacona, Jaramillo (2); Las Tecatas; Los Reyes (181); Tancítaro (10); Uruapan (3).

This toad is an inhabitant of pine and oak forests between 900 and 2400 meters. Near Charapendo on the slopes of the Sierra de los Tarascos and at Coalcomán it apparently reaches its lowest altitudinal limits. At both of these localities the pine-oak forest is replaced by arid tropical scrub forest on the lower slopes.

Twenty-four tadpoles were collected on May 3 in a quiet section of a fast stream near Barranca Seca. The tadpoles have a robust body, broadest about two-thirds the distance from the snout to the posterior edge of the body, half again as broad as deep. Eyes dorsolateral; nostrils dorsal, somewhat directed forward, and about three-fifths the distance from the tip of the snout to the eye; spiracle sinistral and lateral, located at about midbody; anus median; tail long and slender; tail-musculature extends nearly to tip of tail; depth of tail-musculature at mid-length about one-third total depth of tail; dorsal tail-fin not extending onto body (Fig. 5); average body length of ten tadpoles having small hind limb buds, 14.4 mm.; average tail length, 22.0 mm.

Mouth ventral, nearly terminal, about one-third as wide as widest part of body; anterior lip has no papillae; lower lip bordered by two rows of papillae and lateral lips by one row of papillae; beaks moderately well developed, the upper forming a broad arch and

finely denticulate; tooth rows ⅗, the upper rows extending to the edge of the lips, subequal in length, and slightly longer than lower rows, which also are subequal in length; inner upper tooth row broken medially; inner lower tooth row sometimes broken (Fig. 6).

The body is black dorsally and laterally, and bluish gray ventrally; the tail musculature is brown and stippled with darker brown. The fins are transparent and stippled with brown, the stippling being most pronounced on the posterior two-thirds of the upper tail-fin.

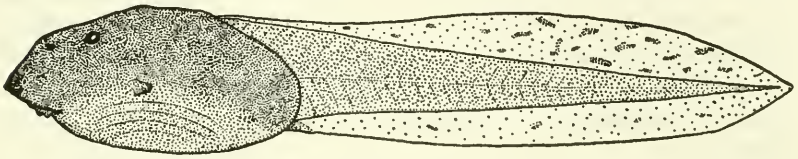


FIG. 5. Tadpole of *Bufo occidentalis* (UMMZ 94269) from Barranca Seca, Michoacán. × 3.

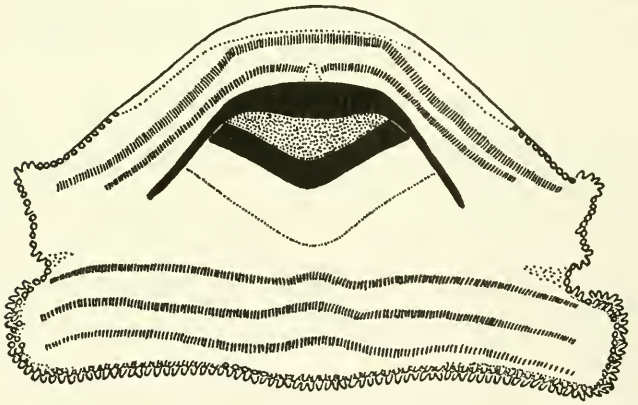


FIG. 6. Mouthparts of larval *Bufo occidentalis* (UMMZ 94269) from Barranca Seca, Michoacán. × 20.

Forty recently metamorphosed individuals average 18.9 mm. in snout-vent length.

The relationships of this toad seem to be with *Bufo bocourti* Brocchi, an inhabitant of pine and oak forests in the uplands of Chiapas and Guatemala. In *Bufo occidentalis* the tympanum usually is indistinct and sometimes completely covered, and it is absent in *bocourti*. *Bufo occidentalis* has a broader interorbital area and relatively shorter and more rounded parotid glands than *bocourti*. The tadpoles of the two species are nearly identical (see Stuart, 1943:12).

Leptodactylus labialis (Cope)

Cystignathus labialis Cope, Proc. Amer. Philos. Soc., 17:90, 1877.—No type locality designated; type locality restricted to Potrero Viejo, Veracruz, México, by Smith and Taylor (1950a:350).

Leptodactylus labialis, Brocchi, Mission Scientifique au Mexique et dans l'Amerique Centrale, pt. 3, sec. 2, livr. 1:20, 1881.

Apatzingán (26); Capirio (5); Cofradía (9); El Sabino (4); Lombardia; Río Tepalcatepec, 27 km. S of Apatzingán (2).

In the Tepalcatepec Valley this frog reaches the northernmost known limit of its range in western México. Although the species is abundant in the valley, it apparently is absent from the coastal lowlands. In the Tepalcatepec Valley *Leptodactylus melanonotus* seems to be more abundant than *labialis*. In the rainy season both species have been heard calling from the same ponds and flooded fields.

There are only slight differences in size between the sexes; measurements of 20 males and eight females are, respectively: snout-vent length, 32.3-39.5 (35.1), 34.1-39.2 (37.2); tibia length, 14.3-17.0 (15.4), 14.9-16.8 (15.8); head width, 11.0-13.6 (12.0), 12.2-13.2 (12.6); head length, 12.8-15.1 (13.3), 12.8-14.6 (13.7).

Leptodactylus melanonotus (Hallowell)

Cystignathus melanonotus Hallowell, Proc. Acad. Nat. Sci. Philadelphia, 12:485, 1861.—Nicaragua. Type locality restricted to Recero, Nicaragua, by Smith and Taylor (1950a:320).

Leptodactylus melanonotus, Brocchi, Mission Scientifique au Mexique et dans l'Amerique Centrale, pt. 3, sec. 2, livr. 1:20, 1881.

Apatzingán (103); Capirio; Charapendo (7); Coahuayana; Cofradía (10); El Sabino (21); La Playa (3); Lombardia (5); Maruata; Nueva Italia (7); Ostula (9); Playa Azul (11); Río Marquez, 10 km. S of Lombardia; Río Marquez, 13 km. SE of Nueva Italia (6); Río Tepalcatepec, 27 km. S of Apatzingán.

This species is widespread in the lowlands of the state; it has been collected up to elevations of 1050 meters in the Tepalcatepec Valley. In the dry season individuals were discovered beneath rocks along streams and in damp arroyos; in the rainy season they were found wherever there was water. Males were heard calling from flooded fields, ditches, rocky streams, and small puddles. The call is a series of individual notes: "woink, woink, woink."

Adult males are noticeably smaller than females; measurements for 20 males and ten females from Apatzingán are, respectively: snout-vent length, 29.6-34.6 (32.3), 36.3-44.1 (40.8); tibia length, 12.6-15.1 (14.0), 16.5-19.0 (17.8); head width, 10.8-11.9 (11.3), 12.6-14.8 (13.7); head length, 11.2-13.2 (11.9), 13.1-14.8 (14.0). Brownish yellow ventral glands are present in some juveniles and in some adults collected in the dry season as well as in the rainy season.

Leptodactylus occidentalis Taylor

Leptodactylus occidentalis Taylor, Trans. Kansas Acad. Sci., 39:349, 1937.—Tepic, Nayarit, México.

Five km. W of Tangamandapio.

On the night of June 11, 1958, this species was calling from a hyacinth-choked ditch. Although numerous individuals were heard, only one specimen was obtained. The frogs were calling from the tangled mat of hyacinths along with *Hyla eximia, Hypopachus oxyrrhinus ovis,* and *Rana pipiens.*

Taylor (1936a:352) characterized this species as follows: "The narrow head, small maximum size (38 mm. for females, 33 mm. for males), the character of the postaxillary and postfemoral glands, the narrower groups of vomerine teeth, clearly distinguish this western Mexican form from the more robust, larger *melanonotus* to the south. The call is likewise fainter and different in quality." Concerning the glands, Taylor (*loc. cit.*) remarked: "There is a possibility that the horny excrescence covering the glands may appear only during the breeding season. This character is quite as strongly marked in females as in males." Bogert and Oliver (1945:324) concluded that the population of *Leptodactylus* in northwestern México could not be distinguished from *melanonotus* in other parts of the country and thus synonymized *Leptodactylus occidentalis* with *melanonotus.* Bogert and Oliver (*op. cit.*: 324) stated that the extent as well as the presence or absence of ventral glands was highly variable in all samples examined by them.

Upon seeing numerous living individuals of *Leptodactylus melanonotus* from many parts of its range in México and individuals of the population of *Leptodactylus* in northwestern México (Nayarit and Sinaloa), I was immediately impressed not so much by the differences in the development of the ventral glands, but by the color of the glands. The differences in color are apparent in freshly preserved specimens. With the exception of *Leptodactylus* from northwestern México, specimens of *melanonotus* from throughout México and northern Central America have yellow or yellowish brown glands. Specimens from northwestern México have black or brownish black glands that are conspicuously darker than those found in *melanonotus.* Examination of 653 preserved specimens of *Leptodactylus melanonotus* from México and Guatemala has failed to reveal specimens with black ventral glands, like those found in specimens from northwestern México, to which the name *Leptodactylus occidentalis* has been applied. Furthermore, in *melanonotus* the glands are less distinct and more extensive than in *occi-*

dentalis; in the latter species glands are absent from the throat and midventral area, where they often are present in *melanonotus* (Fig. 7).

In some individuals of both species collected in the dry season and in some collected in the rainy (breeding) season the glands are absent; the development of these glands, therefore, does not seem to be correlated with breeding. Likewise, the glands are present or absent in either sex, and often as not they are present in juveniles. Presence of the glands, therefore, cannot be correlated either with sexual or ontogenetic development. Since the

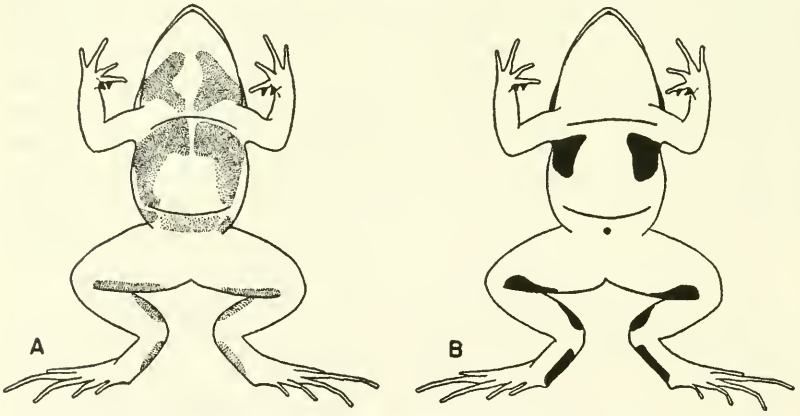


FIG. 7. Diagrammatic view of ventral surfaces of *Leptodactylus melanonotus* (A) and *Leptodactylus occidentalis* (B), showing usual position and size of glandular areas. Approx. natural size.

glands are found in individuals from all parts of the range, it is unlikely that there is a correlation between the development of the glands and the environment.

Aside from the differences in the ventral glands, the call is different in the two populations. The call of *Leptodactylus occidentalis* is a rather harsh "wack, wack, wack" as contrasted with the more nasal "woink, woink, woink" of *melanonotus.* Sound spectographs are needed to analyze the differences in calls. None of the specimens of *occidentalis* examined approaches in size the largest individuals of *melanonotus;* possibly the size of the frogs is another valid character for separating the species. On the basis of the above data it is evident that the frogs in northwestern

México show certain characters that distinguish them from *Leptodactylus melanonotus*, as it is known throughout the rest of México. It is not known for certain that *melanonotus* and *occidentalis* are sympatric. Several series of old, poorly preserved specimens from Nayarit and Sinaloa cannot be placed in either species, for none has visible ventral glands. *Leptodactylus melanonotus* is known from Acaponeta, Nayarit (AMNH 43913-25), and the following localities in Jalisco: Barro de Navidad (UMMZ 118098), La Concepción (UMMZ 113081), La Resolana (UMMZ 102104), and Tenachitlán (UMMZ 113045-6). Records for *Leptodactylus occidentalis* are: Álamos, Sonora (AMNH 51356-65); Culiacán (AMNH 49511-9), Chele (UMMZ 110914), and Rosario (UMMZ 113062) in Sinaloa; Ixtlán del Río (UMMZ 102108), San Blas (UMMZ 112814, 112994, 110892, 115543), and Tepic (UMMZ 115544) in Nayarit; Ameca (UMMZ 102106-7) and La Cofradía on the south shore of Lago de Chapala (UMMZ 102105) in Jalisco; and Tangamandapio, Michoacán (UMMZ 119145). From these scattered records it appears that *Leptodactylus occidentalis* in the southern part of its range stays in the uplands, whereas *melanonotus* is confined to the lowlands.

Microbatrachylus hobartsmithi (Taylor)

Eleutherodactylus hobartsmithi Taylor, Trans. Kansas Acad. Sci., 39:355, 1937.—Uruapan, Michoacán, México.

Microbatrachylus hobartsmithi Taylor, Univ. Kansas Sci. Bull., 26:501, November 27, 1940.

Cascada Tzararacua (6); 21 km. W of Ciudad Hidalgo; 29 km. E of Morelia; Puerto Hondo; San José de la Cumbre (13); Uruapan (2); Zitácuaro.

Of six specimens from Cascada Tzararacua, five are colored like typical *M. hobartsmithi*, having the anterior and posterior surfaces of the thighs and the upper arms pale pink in life and a grayish brown dorsum in preservative. The other specimen (UMMZ 94231) has in preservative a dark brown dorsolateral line on each side enclosing a pale tan area that extends from the snout to the vent. One specimen from 29 kilometers east of Morelia (UIMNH 40338) and 13 specimens from San José de la Cumbre (UMMZ 102111) do not have the prominent tarsal tubercles characteristic of *M. hobartsmithi*. Also, in these fourteen specimens the palmar tubercles are larger, and the dark anal patch more distinct, than in typical *M. hobartsmithi*. Possibly these specimens, which are from the high mountains

in the eastern part of Michoacán, represent another species of *Microbatrachylus*. However, Taylor (1940d:501) reported a series of *M. hobartsmithi* from the mountains 10 miles west of Villa Victoria in the western part of the state of México.

The largest specimen from Michoacán is a gravid female (UIMNH 16104) having a snout-vent length of 23.5 mm.

Microbatrachylus hobartsmithi has been found in rocky ravines along streams in the Cordillera Volcánica and the southwestern escarpment of these mountains at elevations from 1450 to 2750 meters.

Microbatrachylus pygmaeus (Taylor)

Eleutherodacytylus pygmaeus Taylor, Trans. Kansas Acad. Sci., 39:352, 1937.—1 mile north of Rodriguez Clara, Veracruz, México.

Microbatrachylus pygmaeus Taylor, Univ. Kansas Sci. Bull., 26:500, November 27, 1940.

Microbatrachylus albolabris Taylor, Univ. Kansas Sci. Bull., 26:502, November 27, 1940.—2 miles west of Córdoba, Veracruz, México.

Microbatrachylus minimus Taylor, Univ. Kansas Sci. Bull., 26:507, November 27, 1940.—Agua del Obispo, Guerrero, México.

Microbatrachylus imitator Taylor, Univ. Kansas Sci. Bull., 28:70, May 15, 1942.—La Esperanza, Chiapas, México.

Arteaga (328).

This large series (UMMZ 119247-8) was collected on June 22 and 23, 1958, before the onset of the heavy summer rains. The frogs were found in a shaded ravine at the north edge of Arteaga; they were obtained during the day, at which time they were actively moving about in the leaf litter along a small stream.

These frogs are all referred to *M. pygmaeus*, because this is the earliest name available for frogs showing the variation in characteristics displayed by this large series. The characters used by Taylor (1936a, 1940d, 1941a, and 1942b) and Smith and Taylor (1948) to distinguish the various species of *Microbatrachylus* include color pattern, relative length of the hind limb, presence and position of dorsal dermal folds or pustules, relative size of inner and outer metatarsal tubercles, and the number of palmar tubercles. All specimens from Arteaga have two palmar tubercles; the inner and outer metatarsal tubercles are subequal in size. Furthermore, aside from sexual difference, there is little variation in the relative length of the hind limbs (Table 3). However, many color patterns do exist in the series; each of these color patterns is described below.

TABLE 3.—SNOUT-VENT LENGTH EXPRESSED AS A PERCENTAGE OF TIBIA LENGTH IN ANIMALS OF SIX COLOR PATTERNS OF MICROBATRACHYLUS PYGMAEUS. (LETTERS REFER TO THE VARIANTS HAVING THE COLOR PATTERN DISCUSSED IMMEDIATELY BELOW)

COLOR PATTERN	Sex	Number of specimens	Range of variation	Mean	Twice standard error of mean
A	♂	25	51.4–57.5	55.2	3.34
	♀	25	49.3–54.9	51.6	3.12
B	♂	20	51.0–57.1	55.4	2.44
	♀	21	47.3–54.9	51.2	3.52
C	♂	6	54.5–56.2	55.2	.....
	♀	6	50.0–52.9	51.6	.....
D	♂	17	52.9–58.2	55.4	2.64
	♀	14	48.5–56.6	52.1	4.16
E	♂	10	50.9–56.9	55.1	3.40
	♀	7	49.6–54.5	51.6	.....
F	♀	2	51.9–52.6	52.3	.....

A.—225 specimens: Dorsum mottled brown and cream, usually with a dark spot between the eyes and one or two dark V-shaped marks with the apex anteriorly on the back; 55 of these have a narrow cream-colored line from the tip of the snout to the vent and thence onto the posterior surfaces of the thighs. All are pustulate above; in most specimens the pustules form no pattern, but in some they tend to form a V in the scapular region.

B.—41 specimens: Dorsum pale tan or cream-color with brown mottling on flanks; a brown interorbital bar and a brown chevron in scapular region. Dorsum irregularly pustulate; in some specimens the pustules tend to form a V in the scapular region.

C.—12 specimens: Dorsum colored like "A", but having a broad yellow stripe narrowly bordered by black from the tip of the snout to the vent; in some specimens there is a narrow yellow stripe on the posterior surfaces of the thighs. The dorsum is irregularly pustulate.

D.—31 specimens: Dorsum variably streaked with cream-color or pale tan and brown; usually a broad cream-colored stripe from eyelid to groin bordered laterally by a somewhat narrower brown stripe; middorsal area cream-color and separated from dorsolateral cream-colored stripe by a brown stripe, or middorsal area brown with a cream-colored or yellow, narrow stripe from tip of snout to vent; a dark stripe from tympanum to flank; dorsal surfaces of heels creamy white to pale orange; anal patch brown. A dermal ridge from posterior edge of eyelid to rump; another ridge extends posteromedially from the eyelid; scattered pustules on the dorsum in some specimens.

E.—17 specimens: A narrow dark stripe from snout, through nostril and eye, over tympanum, to vent, enclosing a unicolor dorsum (reddish tan to yellowish tan in life); heels pale tan or yellow above; anal patch black. A faint dermal ridge from posterior edge of eyelid to rump, or part way to rump.

F.—2 specimens: Mottled brown and cream-color above; upper lips and

upper arms white. A dermal fold from posterior edge of eyelid to rump; scattered pustules on dorsum.

Some of these color variants are assignable to names proposed by Taylor: "A" and "B" undoubtedly are *M. pygmaeus* (Taylor, 1936a); "C" probably is *M. pygmaeus;* "D" is referable to *M. minimus* (Taylor, 1940d) in most characteristics, although the coloration is more nearly like that of *M. lineatissimus* (Taylor, 1941a), a larger species characterized by a relatively long hind limb; "E" apparently is *M. imitator* (Taylor, 1942b); "F" is *M. albolabris* (Taylor, 1940d). Examination of series of these frogs from other parts of México shows a similar composition of color variants. Of 78 specimens from the Río Sarabia and the village of Sarabia in Oaxaca (UMMZ 115428-37), 57 are "A," six are "D," three are "E," and 12 are "F"; of 22 specimens from Teapa, Tabasco (UMMZ 113829), 11 are "A," five are "D," two are "E," and four are "F"; of 33 specimens from Potrero Viejo, Veracruz (USNM 115447-58, 115461-71, 116840-2, 116864-70), ten are "A," 13 are "E," and ten are "F"; of 31 specimens from La Esperanza, Chiapas (USNM 115477-9, 116827-39, 116849-63), 28 are "A" and four are "F."

It is highly doubtful if these color variants are actually distinct species. Goin (1950 and 1954) in his studies of inheritance of color pattern in West Indian species of the genus *Eleutherodactylus* has shown that similar color pattern variants come from the same clutch of eggs; furthermore, Goin has worked out the genetic ratios of certain of these variants. Heathwole (*in litt.*) obtained "normal" specimens and individuals having a broad middorsal stripe ("C" in figure 9) from a clutch of eggs of *Eleutherodactylus gollmeri.* The presence of a broad middorsal yellow stripe is common in *Eleutherodactylus rugulosus.*

Perhaps the most interesting aspect of variability in color pattern in Mexican eleutherodactylids is the parallelism between members of the *Eleutherodactylus rhodopis*-group and some members of *Microbatrachylus.* In the former group there are white-lipped individuals (*Eleutherodactylus beatae* Boulenger), individuals having a unicolor reddish or yellowish dorsum (*E. dorsoconcolor* Taylor), and individuals having a dorsal pattern of irregular longitudinal brown and cream-colored streaks (*E. venustus* Günther). In the humid forests of southern Veracruz, northern Oaxaca, and Chiapas members of both groups occur sympatrically. A proper understanding of the evolutionary significance of these variants in the two groups, as well as proper allocation of the presently recognized species, must await experimental evidence based on studies

of the inheritance of color pattern. Nevertheless, at present it is apparent that certain characters, especially the nature of the dermal folds and pustules, and the color pattern, are of little taxonomic value in distinguishing "species" of *Microbatrachylus.* The data derived from a study of the large series from Arteaga, together with that from the other series examined, suggests that *Microbatrachylus albolabris, imitator, minimus,* and *pygmaeus* are morphotypes of one species. Of these names, *pygmaeus* is the oldest. Consequently *Microbatrachylus pygmaeus* has been used here for the series from Arteaga.

Although *Microbatrachylus hobartsmithi,* a species distinguished from all of the above by the presence of tubercles on the outer edge of the tarsus, is known from Michoacán northward into Nayarit, *Microbatrachylus pygmaeus* previously has not been known north of Guerrero, where it occurs in habitats similar to that in which it was collected at Arteaga.

Eleutherodactylus augusti cactorum Taylor

Eleutherodactylus cactorum Taylor, Univ. Kansas Sci. Bull., 25:391, July 10, 1939.—20 miles northwest of Tehuacán, Puebla, México.
Eleutherodactylus augusti cactorum, Zweifel, Amer. Mus. Novitates, 1813:20, December 23, 1956.

Cherán; Coalcomán; Uruapan.

The few specimens indicate that this species occurs at moderate to high elevations in the state. The specimens from Cherán and Uruapan were obtained in pine forests; the specimen from Coalcomán was found on a rocky hillside covered with dense forest and located about 100 meters below the lower limits of the pine forest in the area. A specimen from Rancho Reparto (elevation 1850 meters) on the west slope of Cerro Barolosa was lost.

The specimen from Coalcomán (UMMZ 104728) is a juvenile having a snout-vent length of 25.0 mm. In life it was tan above, mottled with olive-green. The ventral surfaces were gray; the hind limbs were distinctly barred with yellow and brown, and the lips were barred with yellow and black.

Eleutherodactylus occidentalis Taylor

Eleutherodactylus occidentalis Taylor, Proc. Biol. Soc. Washington, 54:91, July 31, 1941.—Hacienda El Florencio, Zacatecas, México.

Arteaga (2); Cascada Tzararacua; Coalcomán (2); 19 km. SW of Coire (3); La Placita (7); Los Reyes; Ostula (4); Pómaro (2).

The locality records for this species suggest that it is a member of a group of animals, the distribution of which includes the western part of the Mexican Plateau and the Pacific lowlands. In Michoacán

this frog has been collected in pine-oak forest at Cascada Tzararacua and at Los Reyes, in arid scrub forest at Arteaga and Coalcomán, and in tropical semi-deciduous forest on the lower Pacific slopes of the Sierra de Coalcomán. On July 5, 1950, James Peters (1954:6) found calling males at La Placita.

Most of the specimens are immature; four adult males have snout-vent lengths of 30.9-33.0 (32.2) mm. In all specimens the first finger is noticeably longer than the second; the inner metatarsal tubercle is large, flat, and cream-colored, contrasting with the dark brown sole of the foot. When the hind limbs are adpressed, the heels broadly overlap. Characteristically, a dark line extends from the snout, through the eye, above the tympanum, to a point above the insertion of the forelimb. Usually there is a dark bar behind the tympanum, two dark brown bars from the eye to the mouth and thence onto the lower jaw, and another dark bar on the upper lip between the eye and nostril. One adult from Arteaga, an adult and a juvenile from La Placita, and one juvenile each from Coire, Ostula, and Pómaro, have the lower lip barred with dark brown and white, and have a white stripe extending the length of the upper lip. In life the dorsum varies from dark gray or olive-brown to tan or reddish brown.

This species belongs to a group containing two other populations that are currently recognized as species—*calcitrans,* known only from Omiltemi, Guerrero, and *mexicanus,* reported from the mountains of Oaxaca. Another apparently undescribed member of this group has been collected in the mountains of northern Puebla. The locality records indicate that the group inhabits the mountains on the periphery of the Mexican Plateau, except in western México, where *Eleutherodactylus occidentalis* extends to the Pacific lowlands.

Eleutherodactylus rugulosus vocalis Taylor

Eleutherodactylus vocalis Taylor, Univ. Kansas Sci. Bull., 26:401, November 27, 1940.—Hacienda El Sabino, Michoacán, México.

Arteaga (10); El Sabino (8); Salitre de Estopilas (3); Tumbiscatio (2); Tzitzio (2).

The distributional data on this frog in Michoacán indicate that it inhabits riparian situations in arroyos and canyons in the lower slopes of the Cordillera Volcánica and the Sierra de Coalcomán, where it has been taken at elevations only below 1100 meters.

The dorsal color of living individuals from Arteaga varied from dark gray and olive brown to tan and reddish brown. The iris

was grayish brown. In contrast, individuals from Agua del Obispo, Guerrero, had pale golden eyes; specimens from Matías Romero, Oaxaca, had gold eyes heavily flecked with gray; and individuals from Volcán San Martín, Veracruz, had bronze eyes.

The use of the trinomial here is arbitrary. Frogs of the *Eleutherodactylus rugulosus* group in México (*rugulosus, avocalis,* and *vocalis*) exhibit only slight differences in size, proportions, and coloration (Duellman, 1958c:6). Furthermore, the named populations are allopatric. *Eleutherodactylus rugulosus vocalis,* as defined by Duellman (*loc cit.*), occurs in the foothills of the Sierra Madre Occidental and associated ranges from central Sinaloa southward into Michoacán.

Tomodactylus angustidigitorum Taylor

Tomadoctylus angustidigitorum Taylor, Univ. Kansas Sci. Bull., 26:494, November 27, 1940.—Quiroga, Michoacán, México.

Angahuan (6); Apo; Carapan (21); 19 km. S of Carapan (13); Cerro Tancítaro (12); Cherán; Corupu (14); Cuseño Station (14); Opopeo (3); Paracho (11); Parícutin (2); Pátzcuaro (3); Quiroga (59); San Juan de Parangaricutiro (16); Tancítaro (25); Uruapan (8); Zacapu (11).

This species is indigenous to the pine-oak forests on the southern rim of the Mexican Plateau, and has been collected at elevations from 1500 to 2500 meters. Males have been observed to call from rocks, rock fences, clumps of grass, and low bushes; the call is a single "peep." At San Juan de Parangaricutiro numerous specimens were found in the daytime beneath adobe bricks and lava on the volcanic ash derived from Volcán Parícutin; at Paracho individuals were found by day beneath rocks in a pine forest.

In most specimens the dorsum is dark reddish brown, and the prominent inguinal glands are cream-color or pale orange (Pl. 3, Fig. 1). Of eight individuals collected at Paracho, one was reddish brown, two were pinkish tan, three were dark brown, and two were black.

Tomodactylus fuscus Davis and Dixon

Tomodactylus fuscus Davis and Dixon, Herpetologica, 11:157, July 15, 1955.—1.5 miles southeast of Huitzilac, Morelos, México.

Los Cantiles (2); 28 km. E of Morelia.

The range of this species includes the Sierra Ajusco in México and Morelos and thence westward to the Serranía Ucareo in Michoacán. The specimen from 28 kilometers east of Morelia was found in an oak forest on a steep hillside at an elevation of 2100 meters. One from Los Cantiles was calling from a steep cliff at

an elevation of 2200 meters in pine-oak forest. This specimen (UMMZ 119156) in life had a pale olive-brown dorsum with irregular dark brown mottling and transverse bars on the limbs. The interorbital bar, the upper arms, and the tips of the dorsal pustules were pale orange; the iris was pale grayish gold (Pl. 3, Fig. 2).

Tomodactylus nitidus nitidus (Peters)

Liuperus nitidus Peters, Monats. Akad. Wiss. Berlin, p. 878, 1869.—Izúcar de Matamoras, Puebla, México.

Tomodactylus amulae Günther, Biologia Centrali-Americana, Reptilia and Batrachia, p. 219, April, 1900.—Amula, Guerrero, México.

Tomodactylus nitidus nitidus, Dixon, Texas Jour. Sci., 9:385, December, 1957.

Copuyo (15); Tuxpan (8); Tzitzio (11).

One specimen from Tzitzio (UMMZ 99155) was referred to *Tomodactylus nitidus petersi* by Dixon (1957:390). A re-examination of this specimen, and examination of ten others from the same locality (UMMZ 121571) reveals that the relatively small size of the tympanum and absence of dense ventral spotting place these specimens closer to *T. nitidus nitidus* than to *T. nitidus petersi.*

The specimens from Tuxpan (UMMZ 114303-4) had in life a gray to olive tan ground color with dark olive-green markings, bright yellow thighs with olive-green transverse bands, yellowish tan shanks with olive-green bars, yellow groin, white inguinal glands with black markings, grayish white belly with scattered brownish black spots in some specimens, and a deep golden iris (Pl. 4, Fig. 1). These specimens were found calling from bushes in a rocky field at an elevation of 1800 meters. The call is a high-pitched "pee-ee-eep."

Tomodactylus nitidus orarius Dixon

Tomodactylus nitidus orarius Dixon, Texas Jour. Sci., 9:392, December, 1957.—4.5 miles southwest of Tecolapa, Colima, México.

La Placita (3); Pómaro.

These specimens, referred to *Tomodactylus petersi* by Duellman (1954b:5), were included in *T. nitidus orarius* by Dixon (1957:392). Color notes based on living individuals from Tecolapa, Colima (UMMZ 114312 and 116922), are: gray above mottled with brown; venter dirty white; anterior and posterior surfaces of thighs bright yellow; iris pale golden (Pl. 4, Fig. 2). The call is a soft "braa" usually followed by three high notes: "braaa-eep-ee-eep." In Michoacán this subspecies has been found only in the coastal region and the lower foothills of the Sierra de Coalcomán, an area in which

it replaces *Tomodactylus nitidus petersi.* This is the only *Tomodactylus* known to inhabit coastal lowlands.

Tomodactylus nitidus petersi Duellman

Tomodactylus petersi Duellman, Occ. Pap. Mus. Zool. Univ. Michigan, 560:5, October 22, 1954.—Coalcomán, Michoacán, México.

Tomodactylus nitidus petersi, Dixon, Texas Jour. Sci., 9:390, December, 1957.

Aguililla; Apatzingán (8); Cascada Tzararacua; Charapendo (5); Coalcomán (5); 18 km. E of Dos Aguas (6); El Sabino (5); La Playa (2); Jiquilpan; Uruapan (2); Volcán Jorullo; Zamora.

In life, specimens from Apatzingán (UMMZ 114308-9) varied in dorsal color from grayish tan to pale brown; the dorsal markings were olive green. The thighs and groin were yellowish orange; the iris was pale golden, and the vocal sac was purplish gray (Pl. 5, Fig. 1). Measurements for 13 adult males from the Tepalcatepec Valley are: snout-vent length, 21.9-26.8 (24.3); tibia length, 8.4-9.9 (9.3); head width, 7.2-9.2 (7.8); head length, 7.6-8.7 (8.2).

At Apatzingán and Charapendo in the Tepalcatepec Valley males were found calling from rocks and bushes in open arid tropical scrub forest. The call, a triple note "peep-ee-eep," is repeated once every 90 to 135 seconds. *Tomodactylus nitidus petersi* probably ranges throughout the Tepalcatepec Valley and surrounding foothills. Dixon (1957:392) referred the specimens from Zamora, Jiquilpan, and Uruapan to this subspecies. Uruapan is near the lower limits of the pine forest on the slopes of the Cordillera Volcánica; Zamora and Jiquilpan are on a low part of the Mexican Plateau southeast of Lago de Chapala.

Tomodactylus rufescens Duellman and Dixon

Tomodactylus rufescens Duellman and Dixon, Texas Jour. Sci., 11:78, March, 1959.—Dos Aguas, Michoacán, México.

Dos Aguas (14); 18 km. E of Dos Aguas (6).

Fourteen specimens from the pine-oak forests around Dos Aguas (UMMZ 118503-10, 121498-9) have reddish brown dorsal color and a narrow cream-colored middorsal line (Pl. 5, Fig. 2). Twelve of these specimens are adult males having snout-vent lengths of 20.7 to 24.6 (22.5) mm. One female has a snout-vent length of 24.8 mm., and one juvenile has a snout-vent length of 14.5 mm. Six specimens are from a region of mixture of pine-oak forest and arid tropical scrub forest at 18 kilometers east of Dos Aguas (UMMZ 121497, 121500). All are males having snout-vent lengths of 18.0 to 22.6 (20.7) mm. The dorsum is tan marked with black; the thighs are yellowish orange.

The specimens from 18 kilometers east of Dos Aguas were found on July 22, 1960, by Floyd L. Downs and John Winklemann, who collected calling males of *Tomodactylus rufescens* and *Tomodactylus nitidus petersi* at the same locality. Downs (*personal communication*) stated the call was a single note. At Dos Aguas I heard *T. rufescens* give two calls, one a single "peep," the other a triple note—"pee-ee-eep."

In the higher parts of the Sierra de Coalcomán *Tomodactylus rufescens* seems to fill the same niche as *T. angustidigitorum* does in the Cordillera Volcánica. At lower elevations in their respective mountain ranges the species occur sympatrically with *T. nitidus petersi.*

Diaglena reticulata Taylor

Diaglena reticulata Taylor, Univ. Kansas Sci. Bull., 28:60, May 15, 1942.—Cerro Arenal, Oaxaca, México.

Nueva Italia (3); Ostula (7).

Until recently frogs of the genus *Diaglena* were known only from a few specimens from southern Sinaloa (*Diaglena spatulata*) and from the Pacific lowlands of the Isthmus of Tehuantepec (*Diaglena reticulata*). Peters (1955a) reported specimens from Ostula, Michoacán, and compared these specimens with one *D. reticulata* from Tehuantepec, Oaxaca, and four *D. spatulata* from Sinaloa. This comparison showed that the specimens from Michoacán, although showing some minor differences from *D. reticulata*, are closer to that species than to *D. spatulata.* Subsequent to Peters' work, series of both species of *Diaglena*, including additional specimens from Michoacán and from Colima, have been collected, and a more qualified comparison is now possible.

In comparing specimens of *D. spatulata* from southern Sinaloa (UMMZ 115322) with specimens of *D. reticulata* from Tehuantepec, Oaxaca (UMMZ 115321), the differences noted by Taylor (1942c:60) were found to be constant. But specimens from Ostula, Michoacán (UMMZ 104418), and five individuals from Colima (TNHC 26379-83) were found to be intermediate in certain characters. The skin of the dorsum in *D. reticulata* is granular; that in *D. spatulata* is smooth. The skin in specimens from Ostula and Colima is slightly granular. The dorsal ground color of *D. reticulata* is yellowish brown with dark reticulations; the dorsal ground color of *D. spatulata* is olive-green. Specimens from Ostula and Colima most closely resemble those from Tehuantepec in coloration, but the reticulations are more coarse, and the ground color has an olive-

green tint. *Diaglena reticulata* also differs from *D. spatulata* in having a larger over-all size, slightly broader head, a narrower interorbital distance, and a more pointed snout with a deeper labial shelf (Table 4). The specimens from Ostula and Colima are intermediate between *D. reticulata* from Oaxaca and *D. spatulata* from Sinaloa in body proportions.

Of three specimens from the Tepalcatepec Valley (JRD 5991-3), only two are suitable for measuring. These specimens are smaller than adults from the coastal areas and have broader heads and snouts, but narrower interorbital distances, than specimens in the other samples (Table 4). The texture of the skin is like that of specimens from Ostula and Colima. The coloration resembles that of *D. reticulata*, but the reticulations are bold and form indistinct bands on the hind limbs.

TABLE 4.—COMPARISON OF FOUR CHARACTERS IN FIVE SAMPLES OF DIAGLENA. (ALL DATA ARE FOR MALES; MEANS GIVEN IN PARENTHESES BELOW RANGES.)

LOCALITY	Number of specimens	Snout-vent length	Head width / Snout-vent length	Inter-orbital distance / Head width	Internarial distance / Head width
Oaxaca	9	71.1–87.5 (80.7)	25.4–29.1 (27.9)	63.0–71.4 (67.1)	11.9–13.8 (12.9)
Coast of Michoacán	5	72.0–79.2 (74.8)	24.3–27.2 (25.6)	67.0–73.8 (71.4)	13.7–14.4 (14.1)
Colima	4	71.7–79.6 (74.8)	26.1–28.6 (27.4)	70.5–75.3 (72.0)	16.0–17.9 (16.6)
Tepalcatepec Valley	2	63.0–65.4 (64.2)	28.3–32.2 (30.3)	57.3–62.4 (59.9)	17.0–20.2 (18.6)
Sinaloa	11	71.9–81.3 (77.3)	24.0–27.3 (25.7)	70.5–78.1 (73.4)	15.0–17.3 (16.1)

All specimens from Michoacán and Colima more closely approach *Diaglena reticulata* than *D. spatulata*. The acquisition of additional specimens, especially from the area between Sinaloa and Colima and from Guerrero, is necessary to determine the relationships among the various populations known at present. Both species of *Diaglena* inhabit tropical scrub forest; none has been found in the more humid and tropical semi-deciduous forests. Humid forest replaces the scrub forest in the lowlands of southern Nayarit and

northern Jalisco; possibly this forest acts as a barrier to the distribution of *Diaglena* and thus serves as a divider between the ranges of *D. spatulata* to the north and *D. reticulata* to the south.

Pternohyla fodiens Boulenger

Pternohyla fodiens Boulenger, Ann. Mag. Nat. Hist., ser. 5, 10:326, 1882.—Presidio, Sinaloa, México.

Nueva Italia (2).

These specimens (JRD 5994-5) were found on the road near Nueva Italia during a heavy rain on the night of August 25, 1960, by James R. Dixon. Both are females having snout-vent lengths of 64.0 and 59.0 mm. They are typical of the species as it is known from Sinaloa, Nayarit, Jalisco, and Colima.

These specimens constitute the southernmost record for the species, which ranges in semiarid habitats from southern Arizona southward along the Pacific lowlands of México to Colima and inland on the Mexican Plateau in Jalisco.

Phyllomedusa dacnicolor Cope

Phyllomedusa dacnicolor Cope, Proc. Acad. Nat. Sci. Philadelphia, 16:181, September 30, 1864.—Colima, Colima, México. Funkhouser, Occ. Pap. Nat. Hist. Mus. Stanford Univ., 5:37, April 1, 1957.

Agalychnis alcorni Taylor, Copeia, no. 2:31, June 2, 1952.—Río Tepalcatepec, 17 miles south of Apatzingán, Michoacán, México.

Agalychnis dacnicolor, Duellman, Herpetologica, 13:29, March 30, 1957.

Phyllomedusa alcorni, Funkhouser, Occ. Pap. Nat. Hist. Mus. Stanford Univ., 5:30, April 1, 1957.

Aguililla (13); Apatzingán (7); Charapendo; Coahuayana (3); Coalcomán (54); El Sabino; Huetamo Road (2); La Orilla; La Placita; Nueva Italia (4); 32 km. E of Neuva Italia (2); Río Cancita, 14 km. E of Apatzingán; Río Tepalcatepec, 27 km. S of Apatzingán; Salitre de Estopilas (2); Tzitzio (4).

This large tree frog has been found only in the lowlands below elevation of about 1000 meters, usually in arid tropical scrub forest. Calling males were heard on rainy nights throughout the rainy season; in nearly every instance both males and females were found in low trees and bushes. On summer nights when there had been no rain, adults were found sitting on bushes in the scrub forest.

At Coalcomán on July 1, 1955, a chorus was heard at midday. About forty *Phyllomedusa dacnicolor* were found in one guayava bush at the edge of a recently dried pond. Individual males were calling; clasping males were silent. The call is a barking groan. Fifteen individual egg masses were hanging from branches and leaves in tear-drop fashion. Each egg mass contained 100 to 350 pale green eggs, located only in the exterior part of the clear gela-

tinous mass. Two composite egg masses appeared to have been made up by egg deposition on the part of three to five females (Pl. 2, Fig. 2).

As shown by Duellman (1957a), the characters used by Taylor (1952) to diagnose *Phyllomedusa alcorni* are sexually dimorphic. Funkhouser (1957) apparently was unaware of this sexual dimorphism, for she recognized *P. alcorni* and *P. dacnicolor* as distinct species.

Phrynohyas inflata (Taylor)

Acrodytes inflata Taylor, Univ. Kansas Sci. Bull., 30:64, June 12, 1944.—La Venta, Guerrero, México.

Phrynohyas inflata, Duellman, Misc. Publ. Mus. Zool. Univ. Michigan, 96:19, February 1, 1956.

Phrynohyas corasterias Shannon and Humphrey, Herpetologica, 13:15, March 30, 1957.—4.8 miles east of San Blas, Nayarit, México.

Barranca de Bejuco.

One specimen of this large species was collected in 1951; it was found on a low branch in tropical semi-deciduous forest at an elevation of 65 meters. In life there were olive-gray blotches on a pale gray dorsum; the iris was a dark golden color.

This species, which is known from only a few specimens, seems to be restricted to the coastal lowlands and low foothills from Guerrero northward to Nayarit. Shannon and Humphrey (1957) described *Phrynohyas corasterias* from Nayarit. Their description was based on a small female having a snout-vent length of 34.4 mm. The new species was diagnosed as differing from *P. inflata* in having less webbing on the feet, a poorly developed supratympanic fold, a more pustulate dorsum, and marked differences in dorsal pattern, color, and nature of antebrachial banding. The significance of the webbing was questioned by Shannon and Humphrey. The nature of the supratympanic fold and dorsal pustules changes with age (Duellman, 1956a:31). *Phrynohyas inflata* is known to attain a snout-vent length of 95 mm. Dermal structures that undergo ontogenetic change are of little importance in comparing a juvenile with a large adult. The only significant difference in color pattern between *P. inflata* and *P. corasterias* is the presence of wide transverse bands on the limbs of the latter. In this respect *P. corasterias* approaches *P. latifasciata,* a species known only from two specimens from southern Sinaloa. The acquisition of additional specimens from Jalisco, Nayarit, and Sinaloa may show that *P. inflata* and *P. latifasciata* are conspecific, as suggested by Duellman (1956a:21). Nonetheless, the specimen on which the description of *P. corasterias* was

based is not sufficiently different from the known specimens of *P. inflata* to warrant specific recognition.

Hyla arenicolor

Hyla arenicolor Cope, Jour. Acad. Nat. Sci. Philadelphia, ser. 2, 6:84, July, 1866.—Northern Sonora, México. Type locality restricted to Santa Rita Mountains, Pima County, Arizona, by Smith and Taylor (1950a:354).

Agua Cerca; Cascada Tzararacua (3); Chinapa; Cojumatlán; Dos Aguas; El Sabino (25); El Espinal; Lago de Camécuaro; Lombardia (2); Tupátaro; Zinapécuaro.

Altitudinally this frog ranges from 500 to 2100 meters; although the environments in which it has been found vary from open arid tropical scrub forest to pine forest, it usually is found near rocky streams in these habitats. There is great disparity in size between specimens from the mountains and those from the Tepalcatepec Valley. Seven males from elevations in excess of 1400 meters have an average snout-vent length of 34.7 mm.; nine from elevations below 1000 meters have an average snout-vent length of 49.1 mm. In life a male collected at night at Lombardia (UMMZ 112846) had dark brown spots on a grayish brown dorsum; the groin, anterior and posterior surfaces of the thighs, and ventral surfaces of the hind limbs and palms were yellowish orange. The belly and tips of digits were white; the vocal sac was purplish brown, and the iris was dark grayish gold. In contrast, a specimen obtained in the daytime at Chinapa (UMMZ 119204) had indistinct gray spots on a pale ashy gray dorsum; the flash colors were yellow. After dark the spots were dark olive-brown on a grayish brown dorsum.

Two males were found calling from a rocky stream near Lombardia on July 12, 1955. The call is a nasal "ah-ah-ah-ah."

Hyla baudini Duméril and Bibron

Hyla baudinii Duméril and Bibron, Erpétologie générale, vol. 8:564, 1841. —México. Type locality restricted to Córdoba, Veracruz, México, by Smith and Taylor (1950a:346).

Aguililla (5); Apatzingán (30); Arteaga; Buena Vista; Charapendo; Coahuayana; Cofradía (4); El Sabino (12); La Placita; La Playa; Maruata; Nueva Italia (3); 32 km. E of Nueva Italia (2); Ostula (4); Río Tepalcatepec, 25 km. S of Apatzingán (3); Salitre de Estopilas; San José de la Montaña (2); Tumbiscatio; Tzitzio.

This tree frog is widespread in the coastal lowlands and in the Tepalcatepec Valley up to elevations of about 1200 meters. It is found in numbers in the early part of the rainy season, at which time males were heard calling from bushes and trees along ditches and temporary ponds. The call is a loud nasal "waank-waank-waank." One individual that was emitting a long and unusually

high-pitched call was found to have one hind limb engulfed by a *Leptodeira maculata.*

When active at night these frogs usually are pale tan to reddish brown above with dark brown markings. A specimen found sitting on a maguey plant in the daytime was pale ashy gray with a pale green upper lip.

Hyla bistincta Cope

Hyla bistincta Cope, Proc. Amer. Philos. Soc., 17:87, 1877.—Veracruz, México. Type locality restricted to Acultzingo, Veracruz, México, by Smith and Taylor (1950a:346).

Cerro San Andrés; Dos Aguas (2); Los Conejos (3); Uruapan (50).

In the Parque Nacional at Uruapan this species was found in abundance during the day. The frogs hide in an entanglement of vines and vegetation overhanging several small spring-fed streams. Tadpoles were in the rocky streams, and metamorphosing young were on vegetation at the edges of the streams.

In life the dorsum is greenish tan with brown mottling; in some indivduals the entire dorsum is dark chocolate brown. The flanks are pale lemon yellow barred with lavender-brown. Notes on the color of a living frog from Dos Aguas (UMMZ 119193) are: Dorsal ground color a medium shade of brown with dark brown flecks; flanks black with silvery white and pale yellow spots; belly pale yellowish white; throat mottled with grayish brown; iris pale copper color.

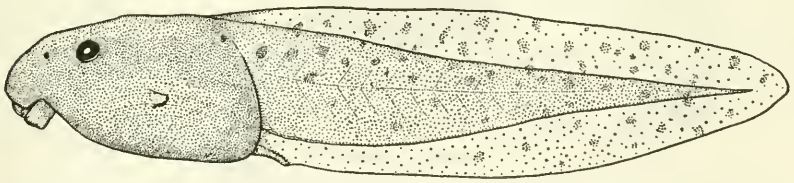


FIG. 8. Tadpole of *Hyla bistincta* (UMMZ 115231) from Uruapan, Michoacán. × 2.

Description of Tadpole: Body somewhat depressed; maximum width of body slightly more than one-half of body length. Nostrils placed dorsolaterally and directed anteriorly, situated about midway between tip of snout and eye. Eyes of moderate size, dorsolateral in position and directed upwards. Tail about twice as long as body, thrice as long as deep, and tapering gradually to a rounded tip. Tail-musculature not extending to tip of tail fin. Spiracle sinistral, lateral, and situated at midbody. Vent dextral;

the cloacal tube extending along ventral part of tail for a distance equal to about one-eighth of body length (Fig. 8). Average body length of six tadpoles with small hind limb buds, 19.5 mm.; tail length, 38.3 mm. Mouth ventral, its width equal to about two-thirds of greatest width of body. Lips bordered by two rows of small papillae; row of larger papillae between upper lip and outer upper tooth-row, similar row between lower lip and outer lower tooth-row; laterally these rows degenerating into numerous small papillae. Horny beaks well developed; upper beak moderately arched and deeply indented; lower beak slightly indented. Serrations of beaks blunt and peglike, moderately developed on both beaks, but slightly stronger on lower one. Tooth-rows 2/3; upper rows nearly equal in length and slightly longer than lower rows, which are subequal in length; inner upper tooth row interrupted medially by rounded notch; inner lower tooth-row turned downward laterally; teeth in all rows about equal in size, but decreasing in length laterally (Fig. 9).

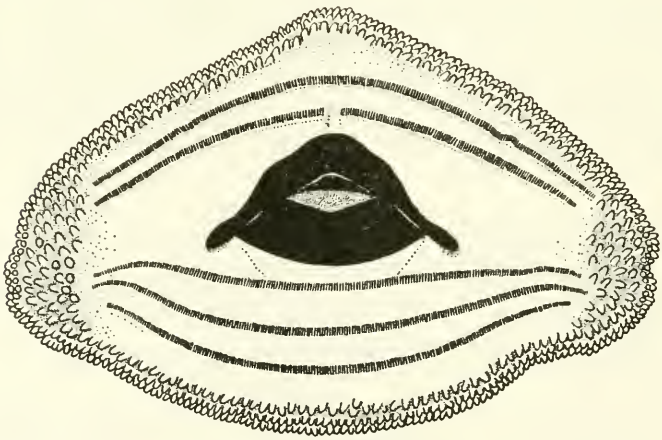


FIG. 9. Mouthparts of larval *Hyla bistincta* (UMMZ 115231) from Uruapan, Michoacán. × 15.

Color in formalin: pale grayish brown dorsally and laterally; pale gray ventrally; tail-musculature brown; tail-fin translucent with scattered melanophores most numerous on upper fin.

In most details these tadpoles resemble those of *Hyla robertsorum* described by Rabb and Mosimann (1955).

Four metamorphosing young have snout-vent lengths of 23.0-

23.5 (23.2); a completely metamorphosed individual has a snout-vent length of 24.8 mm.

In Michoacán this stream-breeding hylid occurs at elevations of 1,600 to 2,400 meters in the Sierra de Coalcomán and in the mountains rising from the Mexican Plateau.

Hyla eximia Baird

Hyla eximia Baird, Proc. Acad. Nat. Sci. Philadelphia, 7:61, October 20, 1854.—Valley of México. Type locality restricted to Coyoacán, Distrito Federal, México, by Smith and Taylor (1950a:329).

Hyla microeximia Maslin, Herpetologica, 13:81, July 10, 1957.—3 miles northwest of Jocotepec, Jalisco, México.

Ciudad Hidalgo (36); Cuitzeo; 29 km. NW of Jacona; Jiquilpan (2); Lago de Camécuaro (2); Lago de Pátzcuaro (129); Los Reyes; Morelia; Sahuayo (3); San Gregorio (63); Tangamandapio (4); Temazcal (26); Tupátaro; Tuxpan (15); Undameo (2); Uruapan (20); Zacapu; Zamora (27); Zinapécuaro (10).

More than 80 per cent of the specimens from Michoacán have brown spots between the lateral and dorsolateral dark stripes, and more than 50 per cent have spots between the dorsolateral stripes, at least posteriorly. In comparison with specimens from the Valley of México, those from Michoacán have more distinct dorsolateral stripes that extend farther anteriorly, sometimes to the eyelid, and in this respect are more nearly like those from Jalisco and Nayarit (Taylor, 1939b:425). Some specimens from the western part of Michoacán possess certain characters used by Maslin (1957:81) to distinguish *Hyla microeximia* from *H. eximia;* nevertheless, the variation is such that two species cannot be distinguished in Michoacán. Four series of freshly preserved specimens have been studied in detail; in the discussion below they are arranged from west to east; the measurement is for snout-vent length of ten males from each sample:

Zamora.—Twenty-two specimens (UMMZ 102083), 24.0-27.6 (26.1) mm. Dorsolateral dark stripe, or row of dashes, present in all specimens; dark spots in lateral and dorsal green fields; lateral dark stripe confluent with dorsolateral stripe posteriorly in 18 specimens; white line not extending to groin.

Temazcal.—Thirty-five specimens (UMMZ 119162), 26.5-31.1 (28.2) mm. Dorsolateral dark stripe of row of spots present only posteriorly in most; both dorsolateral stripes and dorsal spots lacking in four specimens; heavy spotting dorsally in three others; lateral and dorsolateral dark stripes confluent posteriorly in three; lateral white stripe extending to groin in 16 specimens.

Cuidad Hidalgo.—Thirty-six specimens (UMMZ 119163), 26.4-30.9 (28.2) mm. Dorsolateral dark stripe or row of spots present only posteriorly in most; no brown spots in the green fields of many specimens; large brown inguinal spot in most specimens; heavy spotting dorsally in four; lateral and dorsolateral

dark stripes confluent posteriorly in five; lateral white line extending to groin in most specimens.

Tuxpan.—Fifteen specimens (UMMZ 115227), 28.7-33.0 (30.5) mm. Dorsolateral dark stripe or row of dashes in all specimens; dark spots in lateral green fields, at least posteriorly in most; dark spots posteriorly in the dorsal green field in five; lateral dark stripe separated from dorsolateral stripe in all specimens; lateral white line extends to the groin in all specimens.

As can be seen from the above descriptions, the distinguishing characters of *Hyla microeximia*—confluence of lateral and dorsolateral dark stripes posteriorly, extent of lateral white stripe, and distribution of dark spots dorsally—are found in individuals from all of the populations sampled. In the samples from western Michoacán there is a higher incidence of *microeximia*-like frogs than in those from other parts of the state. *Hyla eximia* is a wide-ranging species varying greatly geographically and individually. A thorough review of the species and related members of the *Hyla eximia*-group is necessary before certain populations can justifiably be segregated as subspecies or species.

In Michoacán *Hyla eximia* has been collected in mesquite-grassland, pine-oak forest, and cultivated areas on the Mexican Plateau from 1500 to 2300 meters; apparently it is absent from the Sierra de Coalcomán. This is the most abundant frog on the southern part of the Mexican Plateau; in the rainy season breeding choruses are found in temporary pools and in the marshes adjacent to the permanent lakes.

Hyla lafrentzi Mertens and Wolterstorff

Hyla lafrentzi Mertens and Wolterstorff, Zool. Anz., 84:235, August 25, 1929.—Desierto de los Leones, Distrito Federal, México.

Cerro San Andrés (26); Opopeo (9).

In March, 1949, James A. Peters collected this species at elevations of 2400 to 2800 meters on the west slope of Cerro San Andrés. The frogs were found beneath logs and rocks in a damp canyon in coniferous forest. Among the juveniles in this series is a completely transformed individual (UMMZ 102093) having a snout-vent length of 14.5 mm. Five adults have snout-vent lengths of 36.2-39.5 (38.0) mm. *Hyla lafrentzi* has noticeably longer hind limbs than *H. eximia;* in the former, when the hind limb is brought forward along the body, the tibiotarsal articulation extends to the snout. There are dark transverse bands on the hind limbs; the dorsolateral stripe is broken into an anterior and a posterior segment, and the latter is narrowly bordered by white in most specimens.

Hyla lafrentzi occurs at higher elevations than any other frog in Michoacán; the locality records from throughout the range indicate that it is restricted to pine and pine-fir forests. In these habitats it replaces *Hyla eximia,* which inhabits the lower pine-oak forests and mesquite-grassland on the Mexican Plateau. Ponds are absent at places where *Hyla lafrentzi* has been collected; possibly the eggs are laid in streams.

Hyla smaragdina Taylor

Hyla smaragdina Taylor, Copeia, No. 1:18, March 30, 1940.—6 kilometers east of Cojumatlán, Michoacán, México.

Hylella azteca Taylor, Proc. Biol. Soc. Washington, 56:49, June 16, 1943.—Tepoztlán, Morelos, México.

Cojumatlán (30); Copuyo (7); 18 km. E of Dos Aguas (22); Ostula (8); Pómaro (3); Sahuayo; Salitre de Estopilas (7).

Taylor (1940a:18) diagnosed this species as having few or no vomerine teeth, no vocal sac, a rather broad and flat head, two large tubercles below the anus, a granular venter, and a green dorsum in life. The specimens on which the description was based are either immature or non-breeding individuals; all were collected from bromeliads growing on cacti near Cojumatlán. Another small, flat-headed hylid from Tepoztlán, Morelos, was described and diagnosed by Taylor (1943b:49) as differing from *Hyla smaragdina* in having a vocal sac and a broader head. This specimen was named *Hylella azteca.* Specimens from the coastal region of Michoacán and Colima were referred to *Hylella azteca* by Peters (1954:7) and Duellman (1958c:8).

Comparison of topotypic *Hyla smaragdina* and the holotype of *Hylella azteca* (UIMNH 25044) with the several series of specimens from Michoacán has resulted in the conclusion that all pertain to only one species. Although the type series of *Hyla smaragdina* consists of immature specimens, the males in that series do possess vocal sacs. Since these were not breeding individuals, the sacs are not well developed. The characters of the anal tubercles and the relative width of the head are of no value in separating the two species. The apparently aestivating individuals comprising the type series of *Hyla smaragdina,* and the type of *Hylella azteca,* which also was found in a bromeliad, were green in life. Of the calling males found on the coast of Michoacán, most were yellowish tan when found; two were pale green, but soon changed to pale tan. Calling males from Copuyo and Dos Aguas were pale yellowish tan. Therefore the color of the dorsum is of little significance in distinguishing the two named populations.

Males of *Hyla smaragdina* have been found calling in the months of June and July from rocky streams; the call is a nasal "haah-haah-haah," repeated quickly and constantly for as long as 30 seconds. As pointed out by Duellman (1958c:9), this breeding behavior is unlike that suggested by Taylor (1943b:51). In Michoacán *Hyla smaragdina* has been found in tropical semi-deciduous forest, oak forest, and mesquite-grassland at elevations from 150 to 1500 meters.

Hyla smithi Boulenger

Hyla smithi Boulenger, Zool. Rec. Reptilia and Batrachia, 38:33, 1902.—Cuernavaca, Morelos, México.

Aguililla (14); Apatzingán (104); Arteaga; Charapendo (5); Coalcomán (11); El Sabino (44); La Playa (6); Lombardia (2); Nueva Italia (8); Playa Azul; Salitre de Estopilas (2).

This small hylid is abundant in the Tepalcatepec Valley to elevations of about 1000 meters; it was found infrequently on the coastal lowlands. Males call from bushes in and around flooded fields and ditches, from grasses and small herbs in the water and from vegetation overhanging small streams. The call consists of a series of short, high notes, somewhat reminiscent of a katydid's song. In the dry season occasional males were heard calling from irrigated fields near Apatzingán. In the daytime individuals were found in the axils of leaves of the elephant-ear plants (*Xanthosoma*).

In living individuals the dorsal color usually is uniform pale yellow; often the lateral white stripe is barely visible. The vocal sac is bright yellow, and the iris is pale gold. In some individuals there are scattered dark brown spots or flecks on the back and upper surfaces of limbs. Twenty males from Apatzingán have the following measurements: snout-vent length, 22.8-26.0 (25.0) mm., tibia length, 10.7-13.6 (12.6) mm.; head width, 7.2-8.0 (7.6) mm., head length, 7.1-8.1 (7.7) mm.

Hypopachus caprimimus Taylor

Hypopachus caprimimus Taylor, Univ. Kansas Sci. Bull., 26:526, November 27, 1940.—Agua del Obispo, Guerrero, México.

Buena Vista; Copuyo (6); Charapendo (3); Cofradía; Jaramillo; Jungapeo; San Salvador; Tuxpan.

Specimens of *Hypopachus* from the Balsas drainage in Michoacán have characters consistent with topotypic *H. caprimimus*. Eleven specimens from the southern edge of the Mexican Plateau all have the flanks darker than the dorsum, a distinct and continuous dark stripe from the occiput to the groin, a large dark spot in the inguinal region, and a pair of dark transverse stripes on the thigh and shank

(Pl. 6, Fig. 1). With the exception of three specimens from Charapendo, all have a predominantly brown venter with round, cream-colored spots.

Peters (1954:8) referred specimens from Buena Vista and San Salvador to *Hypopachus oxyrrhinus*. He stated that the specimen (BMNH 1914.1.28.150) from San Salvador had flanks much darker than the dorsum and a well-defined continuous stripe from the occiput to the groin; this specimen has the characters of *H. caprimimus*. The specimen (BMNH 1914.1.28.151) from Buena Vista resembles *H. oxyrrhinus* in some characters, but it is not like *H. oxyrrhinus ovis* on the Mexican Plateau in Michoacán. The specimen has paired transverse stripes on the hind limbs as does *H. caprimimus*, and is here referred to that species.

In Michoacán this species has been collected in arid tropical scrub forest at elevations of 200 to 1800 meters in the northern foothills of the Sierra de Coalcomán, the Tepalcatepec and Tuxpan valleys, and on the lower slopes of the Cordillera Volcánica. Calling males have been found along streams. One specimen from Charapendo was regurgitated by a *Leptodeira maculata*.

Hypopachus oxyrrhinus ovis Taylor

Hypopachus ovis Taylor, Univ. Kansas Sci. Bull., 26:520, November 27, 1940.—Tepic, Nayarit, México.
Hypopachus oxyrrhinus ovis, Shannon and Humphrey, Herpetologica, 14:89, July 23, 1958.

Emiliano Zapata; 30 km. NW of Jacona (2); 10 km. NE of Pátzcuaro (2); Tangamandapio (16); 24 km. W of Zamora (16).

Thirty-seven specimens from the Mexican Plateau in northwestern Michoacán agree well with the diagnosis of *Hypopachus oxyrrhinus ovis* by Shannon and Humphrey (1958). With the exception of one specimen from Tangamandapio, all have dark bellies extensively mottled or spotted with cream-color. Most of the specimens have some form of an irregular, usually broken, dark line from the occiput to the groin. In eight specimens there is no line or linear arrangement of spots; instead the dorsum is spotted or flecked with dark brown. The ground color of the dorsum and flanks varies from dull reddish brown to grayish brown; cream-colored spots are evident on the flanks and posterior surfaces of the thighs in all specimens (Pl. 6, Fig. 2).

In comparison with 14 specimens from Quesería, Colima (UMMZ 80001-2), individuals from the Mexican Plateau have a

darker venter with bolder markings, and a more mottled dorsum.

In Michoacán this species has been taken between 1500 and 2200 meters on the Mexican Plateau, where it inhabits mesquite-grassland and cultivated areas.

Rana dunni Zweifel

Rana dunni Zweifel, Copeia, no. 2:78, July 15, 1957.—Lago de Pátzcuaro, Michoacán, México.

Lago de Pátzcuaro (23); Río de Morelia, near Undameo (8).

Aside from the type series of this species, there are in the Museum of Zoology at the University of Michigan six specimens taken from "tanks" at the limnological station at Pátzcuaro by Paul S. Martin in 1948, and eight specimens found in shaded ditches along the Río de Morelia by Robert R. Miller on April 4, 1957. The Río de Morelia flows into Lago de Cuitzeo; this drainage is separated from Lago de Pátzcuaro by a chain of hills about 2400 meters in elevation. Dr. Richard G. Zweifel has examined these specimens and has informed me that, although they differ slightly from typical *Rana dunni*, they are much closer to that species than to *Rana montezumae*.

Rana megapoda Taylor

Rana megapoda Taylor, Univ. Kansas Sci. Bull., 28:310, November 12, 1942.—Chapala, Jalisco, México.

La Palma (8).

These specimens (USNM 113998-114005) are from the marshes along the southeastern shore of Lago de Chapala. Five females have snout-vent lengths of 124.0-138.1 (131.5), and one male has a snout-vent length of 110.2 mm. Two juveniles have snout-vent lengths of 49.7 and 56.3 mm. The coloration of the juveniles is more bold than that of the adults. The body proportions of these specimens agree with those presented by Zweifel (1957:80).

Rana montezumae Baird

Rana montezumae Baird, Proc. Acad. Nat. Sci. Philadelphia, 7:61, October 20, 1854.—Mexico City, Distrito Federal, México.

La Palma; 8 km. NW of Maravatio (10); Sahuayo; Tupátaro (7).

This species probably is more abundant and widespread than is indicated by the few specimens listed above. It has been found only in the vicinity of permanent water on the Mexican Plateau and the mountains rising from the plateau at elevations of 1500

to 2000 meters. Its apparent absence from Lago de Pátzcuaro cannot be explained, unless *Rana dunni* replaces it there.

Rana pipiens Schreber

Rana pipiens Schreber, Der Naturforscher, Halle, 18:185, 1782.—Raccoon, Gloucester County, New Jersey.

Aguililla (2); Apatzingán (13); Arteaga; Axolotl (16); Camachines (2); Capirio; Cascada Tzararacua (3); Cerro San Andrés (6); Charapendo (4); Ciudad Hidalgo; Coalcomán (17); Cuitzeo (3); El Sabino (10); Jacona (3); 29 km. NW of Jacona (8); Jiquilpan; La Orilla (3); La Palma (5); La Playa (4); Lago de Chapala (3); Lago de Pátzcuaro (6); Lombardia; Los Conejos (67); Los Reyes (7); Macho de Agua; Maravatio; Morelia (5); Opopeo (3); Pátzcuaro (9); 26 km. S of Pátzcuaro (52); Puerto Hondo (3); Río Duero, 14 km. E of Zamora (13); Río Tepalcatepec, 27 km. S of Apatzingán (2); San Gregorio (38); San José de la Cumbre (5); Tangamandapio; Zacapu; 18 km. W of Zamora (35).

Except on the Pacific lowlands, this species is abundant throughout the state. It has been collected from sea level to 2800 meters, the greatest altitudinal range of any amphibian in Michoacán. It has been found frequently in the Tepalcatepec Valley; it is not a distinctly highland species in southern Michoacán, as stated by Peters (1954:9). One specimen from Aguililla (UMMZ 119257) is an albino. In this specimen there is a faint pattern on the hind limbs; otherwise the entire body is creamy white; the eyes are pink.

Rana pustulosa Boulenger

Rana pustulosa Boulenger, Ann. Mag. Nat. Hist., ser. 5, 11:343, 1883.—Ventanas, Durango, México.

Arteaga (4); 21 km. S of Arteaga; Cascada Tzararacua (3); Coalcomán (3); 12 km. ENE of Dos Aguas (3); El Sabino (53); Los Reyes (3); Tzitzio (4); Uruapan.

Although *Rana pustulosa* seems to be absent from the Mexican Plateau in Michoacán, it has been collected at elevations of 850 to 2150 meters on the slopes of the Cordillera Volcánico and in the Sierra de Coalcomán. Usually the frogs are found along rocky streams, but at Coalcomán they were found in a hyacinth-choked old river channel, and at El Sabino, in irrigation ditches.

In most specimens the dorsum is dark olive-brown; in some it is pale olive-tan with dense dark brown mottling on the back and dark transverse bands on the hind limbs.

Thirteen tadpoles (UMMZ 94271) taken from a seepage pool by a stream near Uruapan closely resemble the description of tadpoles of this species given by Taylor (1942b).

REPTILIA

Testudines

Chelonia mydas (Linnaeus)

Testudo mydas Linnaeus, Systema naturae, ed. 10:197, 1758.—Type locality restricted to Ascension Island by Mertens and Müller (1928:23).
Chelonia mydas, Brongniart, Bull. Sci. Soc. Philom., 2:89, 1800.

Beach between Río Motín and Río Colotlán (2); Maruata; Playa Azul (4).

Green sea turtles are abundant along the coast of Michoacán. Laying females and fresh nests were found on August 6-12, 1950, July 14-16, 1951, and July 8-10, 1955. The general account of sea turtles on the coast of Michoacán that was given by Peters (1957) is supplemented here by my field notes on the actions of one female observed on the night of July 14, 1951, near Maruata by Donald D. Brand and I. Because of a full moon, visibility was excellent.

In the course of the day several *Chelonia* were seen in the surf; shortly after dark the first turtle was observed on the beach. Several were observed to come out on the beach and crawl nearly to the strand line, only to return to the sea.

At 10:20 p. m. one turtle was seen about 15 meters from the water. We watched this turtle from some distance and observed that by 10:26 p. m. she had moved about ten meters to a bank of sand about two meters high. Ten minutes later she had climbed the bank and disappeared over the top into the brush. We moved closer and remained hidden below the bank. Although we could not see the turtle, we could hear her movements. Between 10:37 and 10:57 p. m. the turtle dug, often flipping the dry sand for a distance of about two meters. When this energetic digging ceased, we moved up the bank to see that she was facing inland and sitting in a depression about one and one-half meters in diameter and 30 centimeters in depth. She had cleaned out this depression in the past 20 minutes. Between 11:00 and 11:36 p. m. she dug the nest hole by first scooping sand with one hind flipper and then with the other; when sand was thrown by one flipper, there was a similar, but weaker, motion by the other flipper. At 11:36 p. m. she stopped digging. By crawling up behind the turtle we were able to examine the nest cavity, which measured 21 centimeters across the top and 38 centimeters deep. The diameter of the bottom of the hole was estimated to be about 50 centimeters. At 11:40 p. m. she released the first egg; a minute later she dropped the second. At 11:42 p. m. the third and fourth eggs were released; these were coherent, as were the fifth and sixth eggs released at 11:43 p. m. After this, as many as three eggs

were dropped at a time. After laying about 60 eggs, she paused for a minute and then continued laying. By 11:55 p. m. she had laid 98 eggs; after this, the process of deposition slowed considerably. She dropped a fragment of an egg followed by normal eggs. At midnight she deposited a miniature egg about 20 mm. in diameter. This terminated the deposition. Immediately she began to cover the nest.

Within ten minutes after the last egg was deposited the nest had been covered. The turtle first had been seen at 10:20 p. m.; judging from its speed and its distance from the water, the turtle probably had been on land for about ten minutes. About 25 minutes were used in crawling from the water to the nesting site. One hour and 33 minutes were spent at the nesting site; of this time twenty minutes were taken for egg deposition. The turtle was not followed back to the water, but if the return trip took approximately the same amount of time as required to travel from the ocean to the nesting site, the total elapsed time from departure to return to the water was about two and one-half hours.

We collected the eggs as they were deposited. There were 106 eggs, each having a diameter of about 40 mm., plus one small egg and a fragment of another. The turtle had a carapace about one meter in length.

From our limited observations of sea turtles and their tracks on the beaches, and from the accounts of these animals by the residents of the coastal region, great numbers of sea turtles use these relatively uninhabited beaches for nesting grounds. However, the turtles do not go unmolested. The natives capture turtles and collect their eggs. Opened and emptied nests also showed signs of predatory activity on the part of other mammals. In the vicinity of Playa Azul several turtles were killed by dogs.

Kinosternon hirtipes hirtipes Wagler

Cinosternon hirtipes Wagler, Naturl. Syst. Amph., p. 37, 1830.—México. Type locality restricted to Mazatlán, Sinaloa, México, by Smith and Taylor (1950b:25).

Kinosternon hirtipes hirtipes, Schmidt, Check list N Amer. Amph. Rept., ed. 6, p. 89, 1953.

Eight km. W of Ciudad Hidalgo; Jiquilpan; La Palma; Lago de Camécuaro (4); Lago de Cuitzeo (3); Lago de Pátzcuaro (8); 14 km. E of Zamora (4).

One specimen from eight kilometers west of Ciudad Hidalgo (UIMNH 24707) is from the Río Tuxpan, a tributary of the Río Balsas; this is the only record for the species from the Balsas drainage. All others are from the lakes or rivers flowing into the lakes on the southern part of the Mexican Plateau. This species exists

in Lago de Pátzcuaro to the apparent exclusion of the abundant and widespread *Kinosternon integrum.*

Kinosternon integrum LeConte

Kinosternon integrum LeConte, Proc. Acad. Nat. Sci. Philadelphia, 7:183, 1854.—México. Type locality restricted to Acapulco, Guerrero, México, by Smith and Taylor (1950b:25).

Agua Cerca (3); Aguililla; Arteaga (8); Apatzingán (7); Barranca de Herradero; Buenavista (20); Capirio (2); Charapendo (3); Chupio; Coahuayana (2) Coalcomán (169); Copuyo (4); El Sabino (8); Jacona; Jiquilpan (12); La Orilla (2); La Playa (2); Lago de Cuitzeo (27); Las Higuertas; Lombardia (3); Los Reyes (5); Morelia; Ojos de Agua de San Telmo; San Pedro Naranjestila; Tacícuaro.

Excepting Lago de Pátzcuaro, *Kinosternon integrum* occupies all permanent and temporary ponds, lakes, and streams below 2200 meters throughout the state. At Coalcomán the species was in roadside ditches, small puddles, flooded fields, a hyacinth-choked ox-bow of the Río Coalcomán, as well as in the Río Coalcomán and its tributaries. Specimens from Arteaga and Barranca de Herradero were found in clear rocky streams; the one from Las Higuertas was found in a small muddy pond in pine-oak forest.

On August 26, 1960, James R. Dixon found a copulating pair in a pool at Capirio. The large series from Coalcomán contains juveniles and adults; these turtles formed the basis for the study of relative growth of plastral scutes in this species by Mosimann (1956).

Geoemyda rubida perixantha Mosimann and Rabb

Geoemyda rubida perixantha Mosimann and Rabb, Occ. Pap. Mus. Zool. Univ. Michigan, 548:1, November 9, 1953.—Eight kilometers south of Tecomán, Colima, México.

Apatzingán (2); Coahuayana; La Placita; Punta San Juan de Lima.

These specimens have been discussed in detail by Mosimann and Rabb (1953). All are from the arid tropical scrub forest; those from the coastal regions were collected at elevations of less than 40 meters, and those from the Tepalcatepec Valley were collected at an elevation of 335 meters.

Crocodilia

Crocodylus acutus acutus Cuvier

Crocodylus acutus Cuvier, Ann. Mus. Hist. Nat. Paris, 10:55, 1807.—Santo Domingo.

Crocodylus acutus acutus, Müller and Hellmich, Ibero-Amerik. Stud., 13: 128, 1940.

Boca de Apiza (2); Playa Azul (2).

The crocodile or "caiman" is abundant in the brackish lagoons along the cost of Michoacán; three large adults and several juveniles

were observed at Estero Pichi at Playa Azul; others were seen at Mexiquillo and Maruata. Residents of the Balsas-Tepalcatepec Basin frequently have reported "caimanes" in the Río Balsas and Río Tepalcatepec, but the existence of the crocodile in these rivers has not been verified by specimens.

Sauria

Phyllodactylus duellmani Dixon

Phyllodactylus duellmani Dixon, Southwest Nat., 5:37, April 15, 1960.—Rancho El Espinal, Michoacán, Mexico.

Fourteen km. SSW of Apatzingán; Capirio; Cafradía (3); El Espinal (3).

This species is known only from the Tepalcatepec Valley, where it has been found in open arid situations from 180 to 500 meters. Specimens were found in the daytime in stumps, dead cacti, and the hollow branches of the legume, *Apoplanesia paniculata*. In life adults were pale gray or grayish tan above and creamy white below. A juvenile having a snout-vent length of 18 mm. had a pale orange tail with gray cross-bands. In the adults the tail was colored like the body. The specimen from 14 kilometers south-southwest of Apatzingán (KU 29764) and those from Cofradía (BMNH 1914.1.28.28-30) were not listed by Dixon (1960).

Phyllodactylus homolepidurus Smith

Phyllodactylus homolepidurus Smith, Univ. Kansas Sci. Bull., 22:121, November 15, 1935.—Five miles southwest of Hermosillo, Sonora, México.

El Ticuiz (2); La Placita; Ostula (2); Pómaro; San Pedro Naranjestila.

These specimens have been referred to *Phyllodactylus homolepidurus* by James R. Dixon (*in litt.*), who is currently studying the American members of the genus. Geckos of this species have been found in tropical semi-deciduous forest in the coastal lowlands to elevations of 500 meters. Most specimens were found beneath the bark of standing dead trees or stumps. Two individuals from El Ticuiz (UMMZ 115102) in life were dark gray above with brownish tubercles; the belly was a dusty cream-color. Apparently this species does not enter the Tepalcatepec Valley, where *Phyllodactylus lanei* is abundant.

Phyllodactylus lanei Smith

Phyllodactylus lanei Smith, Univ. Kansas Sci. Bull., 22:125, November 15, 1935.—Tierra Colorado, Guerrero, México.

Apatzingán (13); 21 km. S of Arteaga; El Sabino (53); La Playa; Ostula (2); Río Marquez, 10 km. S of Lombardia (8); 16 km. N of Tafetán.

This widespread species has been taken at elevations of less than 1100 meters in the Balsas-Tepalcatepec Basin, where it occurs in

riparian situations in the foothills. Specimens have been collected in tropical semi-deciduous forest at Ostula and in oak forest south of Arteaga; both of these localities are on the Pacific slopes of the Sierra de Coalcomán, a region inhabited by *Phyllodactylus homolepidurus*. Both species have been collected at Ostula.

A juvenile from 21 kilometers south of Arteaga (UMMZ 118933) had alternating black and white bands on the tail. In life most of the lizards are dull ashy gray or grayish tan above and white below. According to Dixon (*in litt.*), one specimen from Apatzingán (UMMZ 115102) resembles *Phyllodactylus magnus* in scutellation, but it lacks the distinctive yellow venter of that species.

Apparently *Phyllodactylus lanei* is restricted to rather mesic environments in the Balsas-Tepalcatepec Valley and surrounding foothills; in the more open arid environments on the floor of the valley it seems to be replaced by *Phyllodactylus duellmani*.

Phyllodactylus paucituberculatus Dixon

Phyllodactylus paucituberculatus Dixon, Southwest. Nat., 5:40, April 15, 1960.—Río Cupatitzio (= Río Marquez), 6.5 miles south of Lombardia, Michoacán, México.

Río Marquez, 10 km. S of Lombardia (6).

Two of these specimens (UMMZ 112692-3) were discussed in detail by Dixon (1960:40) in his description of the species. On August 25, 1960, Dixon collected four additional specimens at the type locality, a conglomerate cliff along the Río Marquez. These will be reported by him in his forthcoming study of the genus.

Anolis dunni Smith

Anolis dunni Smith, Copeia, no. 1:9, May 10, 1936.—Agua del Obispo, Guerrero, México.

Arteaga (3); 19 km. S of Arteaga.

Three females from Arteaga (UMMZ 119075) have snout-vent lengths of 41, 41, and 44 mm. In life the pale grayish brown dorsum was marked with dark brown; the belly was white, and the throat was pale pink. All have a dark interorbital bar and dark vertical bars on the upper labials. In two specimens there are only scattered dark flecks on the dorsum; in the third there is a dark postorbital stripe, a dark lateral stripe, and four narrow transverse bands on the body. A male from 19 kilometers south of Arteaga (UMMZ 119076) having a snout-vent length of 49 mm. had in life a tan dorsum, a broad white stripe from the ear to the groin, scattered small white spots on the dorsum, and indistinct pale cream-colored spots on the posterior surfaces of the thighs. This male has the dark labial bars,

but lacks the dark interorbital bar, found in the females. The large rose-pink throat fan extends to about the middle of the belly. In all of the specimens the middorsal scales are keeled and much smaller than the smooth pavementlike or slightly imbricate ventrals. All have two gulars in contact with the mental, five scales between the nasals, five scales (not including the first labials) in contact with the rostral, and four rows of loreals. In these characters these specimens agree well with *Anolis dunni* from Guerrero, as diagnosed by Davis (1954b).

Previously *Anolis dunni* has been reported only from the vicinity of Agua del Obispo, Guerrero, a locality situated at an elevation of about 900 meters in pine-oak forest in the Sierra del Sur. All known close relatives of *Anolis dunni* occur only in Guerrero: *A. taylori* Smith and Spieler from Acapulco, *A. gadowi* Boulenger from Tierra Colorado, *A. liogaster* Boulenger, and *A. omiltemanus* Davis from Omiltemi. The present specimens from elevations of about 900 meters in riparian stream vegetation and oak forest represent the northern known limits of this group of *Anolis*.

Anolis nebulosus (Wiegmann)

Dactyloa nebulosa Wiegmann, Herpetologia Mexicana, p. 47, 1834.—México. Type locality restricted to Mazatlán, Sinaloa, México, by Smith and Taylor (1950b:66).

Anolis nebulosus, Bocourt, Mission Scientifique au Mexique et dan l'Amerique Centrale. Reptiles, livr. 2:77, 1873.

Acahuato (3); Agua Cerca; Apatzingán (4); Araparicuaro (3); 29 km. S of Ario de Rosales (3); 20 km. S of Arteaga (2); Barranca de Bejuco; Cascada Tzararacua (5); Cerro Tancítaro (13); Cherán; Chupio (5); Coalcomán (10); Cofradía; Dos Aguas (10); 18 km. E of Dos Aguas (3); El Diezmo; El Sabino (43); El Ticuiz; Jiquilpan (2); La Orilla; La Placita; La Playa (3); Los Conejos (2); Los Pozos; Nogueleras (2); Ostula; 8 km. W of Pátzcuaro (2); 8 km. NE of Pátzcuaro; Playa Azul (3); Río Cachán; Río Marquez, 10 km. S of Lombardia; Río Tepalcatepec, 27 km. S of Apatzingán; San Juan de Lima (6); San Pedro Naranjestila; Temazcal; Tuxpan (2); Tzitzio; Uruapan (74); 11 km. N of Uruapan (2); Volcán Jorullo; 16 km. E of Zacapu (2); 18 km. W of Zamora; Ziracuaretiro.

Even with the abundance of material the assignment of a specific name to these anoles is only tentative, for definite determination between *Anolis nebulosus* Wiegmann and *A. nebuloides* Bocourt is uncertain. Bocourt (1873:75) distinguished *A. nebuloides* from *A. nebulosus* by the following characters: (1) head scales keeled, not smooth; (2) snout narrower; (3) ear opening larger; (4) supraorbital semicircles separated by a row of small scales and not in contact; (5) dorsal scales larger and subequal in size to the belly scales. Boulenger (1885:77) used the same characters; Smith and Taylor (1950b:58) in their key to the Mexican species

of *Anolis* stated that the dorsal scales are slightly smaller than the ventrals in *A. nebulosus* and markedly smaller in *A. nebuloides.* Smith (*in litt.*) stated that the characters of the relative sizes of the dorsal and ventral scales were incorrect in that key.

The application of the above criteria to specimens from Michoacán has not resulted in the recognition of two species. The majority of the specimens have the supraorbital semicircles separated by at least one small scale; the head scales, with the exception of those on the snout in a few individuals, are smooth; the dorsal scales are only slightly smaller than the ventrals. In other characters of scutellation the specimens are highly variable. The males in life have an orange throat fan. Anoles of this kind have been found in Michoacán, Colima, Jalisco, Nayarit, and southern Sinaloa. Near Oaxaca, Oaxaca, specimens were collected that superficially resemble those from Michoacán and farther north. These have low keels on the snout scales, dorsals somewhat larger than the ventrals, and a pink throat fan. In ten males from Oaxaca the size of the dorsal scales relative to that of the ventrals is 1.00 : 0.83; the same ratio for 25 males from Michoacán is 1.00 : 1.08. In both samples there are specimens in which the dorsal and ventral scales are about equal in size.

Investigations by Richard E. Etheridge on the osteology of *Anolis,* including those species here being considered, have revealed relatively constant differences in the parasternalia and in the caudal vertebrae. The application of Etheridge's findings to anoline systematics must await the completion of his study.

The carination of the scales on the snout *versus* smooth scales there seems to be the only significant character given by Bocourt that distinguishes *A. Nebuloides* from *A. nebulosus.* The difference in the color of the throat fan, which is apparent only in living individuals, is more striking. Obviously more than one species is represented, as is borne out by the differences in the color of the throat fan and in the osteology, but there is uncertainty about the correct name for each species. On the strength of Bocourt's diagnosis of keeled snout scales in *A. nebuloides,* I am applying that name to the population in Oaxaca and *A. nebulosus* to the specimens from Michoacán. As arranged here, the two species can be distinguished, as follows:

A. nebulosus.—Dorsal scales only slightly smaller than the ventral scales; snout scales usually smooth; throat-fan bright orange in adult males.

A. nebuloides.—Dorsal scales somewhat larger than the ventral scales; snout scales having a low keel; throat-fan pink in adult males.

With respect to geographic distribution, *A. nebulosus* has been collected from southern Sinaloa southward to Michoacán. The lizards here referred to *A. nebuloides* have been taken only in pine-oak forest on the mountain slopes near Oaxaca City. Zweifel and Norris (1955:233) reported anoles with pink throat-fans from southern Sonora; possibly those specimens are *A. nebuloides;* I have not examined them. I have seen several preserved specimens from the vicinity of Tehuantepec, Oaxaca. Although they probably belong to this group, those specimens differ from both *A. nebulosus* and *A. nebuloides* in their larger size, relatively larger head, and much larger throat fan.

Aside from the minor variation in scutellation, specimens of *Anolis nebulosus* from Michoacán vary greatly in coloration. Usually the females have some form of a broad middorsal pale-colored band. In life this is dull yellow, tan, or orange. Two females from Dos Aguas are strikingly different; one (UMMZ 119521) has a broad middorsal orange stripe that is scalloped laterally and bordered by gray. The other (UMMZ 119081) has a narrow middorsal cream-colored line. Males usually are unicolor brown or olive-tan; sometimes the middorsal region is darker. Some individuals have dark cross-bands or chevrons on the dorsum. One male from Dos Aguas (UMMZ 119080) has a cream-colored lateral stripe.

In Michoacán *Anolis nebulosus* occurs from sea level to elevations slightly in excess of 2100 meters, usually in areas of dense cover, whether this be herbaceous, viney, or woody, ordinarily on the ground as well as in bushes and trees. One was in a bromeliad growing about ten meters above the ground. In the arid Tepalcatepec Valley anoles of this species are most frequently found in the tangled growth along streams. Above Uruapan they were found in pine-oak forest, and on the Mexican Plateau between Zamora and Zacapu they were found in a bunch grass-scrub oak association.

Anolis schmidti Smith

Anolis schmidti Smith, Publ. Field Mus. Nat. Hist., zool. ser., 24:21, January 30, 1939.—Manzanillo, Colima, México.

La Placita; San Juan de Lima.

Peters (1954:11) reported on the specimen from La Placita; another was secured at San Juan de Lima in 1956. The latter (UMMZ 115078) is a male having a snout-vent length of 43.0 mm. and a tail length of 70.5 mm. The dorsal ground color is pale tan; there are five pairs of irregular dark brown dorsolateral blotches. In life the throat fan was pale orange. These specimens agree with those from

Colima described by Duellman (1958c:10). The distribution of *Anolis schmidti* seems to be restricted to the coastal lowlands from Michoacán to Nayarit.

Basiliscus vittatus Wiegmann

Basiliscus vittatus Wiegmann, Isis von Oken, 21:373, 1828.—México. Type locality restricted to Veracruz, Veracruz, México, by Smith and Taylor (1950b:72).

Apatzingán (9); Capirio; Coahuayana (5); El Cerrito; El Sabino (2); El Ticuiz; La Placita (3); Maruata (2); Motín del Oro; Ostula; Playa Azul (3).

This species has been found only on the coast and in the low Tepalcatepec Valley. In the latter area it is restricted to riparian situations along the larger streams. The lizard is abundant in the mangrove swamps bordering the brackish lagoons on the coast. In July, 1955, scores of individuals were seen around Estero Pichi at Playa Azul. Adults, especially the large males, are exceedingly wary and difficult to collect. At all localities where they were found, the lizards were most often seen in dense bushes, where they are well camouflaged. Individuals of all sizes were observed to run across the surface of the ponds.

Iguana iguana rhinolopha Wiegmann

Iguana rhinolopha Wiegmann, Herpetologia Mexicana, p. 44, 1834.—México. Type locality restricted to Córdoba, Veracruz, México, by Smith and Taylor (1950b:72).

Iguana iguana rhinolopha, Van Denburgh, Proc. Acad. Nat. Sci. Philadelphia, 1897:461, January 18, 1898.

Apatzingán (8); Capirio (3); El Cerrito; El Ticuiz (2); La Placita; La Playa (2); Maruata; Playa Azul; Río Cachán.

Like the preceding species, this lizard is always found near water. It does not ascend the foothills of the Sierra de Coalcomán, but in the Balsas Basin it reaches elevations of 800 meters at La Playa. Large adults are often seen in the large trees making up the gallery forests along rivers. From high perches the lizards drop into the water with a terrific splash. Bright green juveniles were abundant in bushes along the Río Tepalcatepec in July, 1955.

Ctenosaura pectinata (Wiegmann)

Cyclura pectinata Wiegmann, Herpetologia Mexicana, p. 42, 1834.—México (by inference). Type locality restricted to Colima, Colima, México, by Bailey (1928:25).

Ctenosaura pectinata, Gray, Catalogue of the lizards . . . British Museum, p. 191, 1845.

Apatzingán (27); between Ario de Rosales and La Playa; Barranca de Bejuco; Capirio (2); Coalcomán (4); El Espinal; El Sabino (2); El Ticuiz; Jazmin (2); La Huacana; La Placita (8); La Playa (3); Limoncito; Lombardia; Motín del Oro; Playa Azul; Río Cancita, 12 km. E of Apatzingán (2); Río Marquez, 10 km. S of Lombardia (2); ? Uruapan; Volcán Jorullo.

Ctenosaura pectinata is a common lowland species that ascends the slopes of the Sierra de Coalcomán and the Cordillera Volcánica to elevations of about 1050 meters (approximating the lower limits of the oak forest). The record from Uruapan (USNM 10234, collected by Dugès) is doubtful.

These large lizards are most easily observed on rock fences along roads. Near Apatzingán innumerable individuals can be seen in mid-morning. Later in the day, as the sun rises higher in the sky, the lizards retreat to the shade of the crevices in the fences. The abundance of these lizards in the Tepalcatepec Valley, together with evidence gathered from the natives of the valley, indicates that these lizards are seldom used for human consumption there. On the other hand, several people in Coalcomán consider the "iguana negra" (local name for *Ctenosaura*) to be a delicacy and serve it at every opportunity. In early July, 1951, brilliant green young of the year were collected at La Playa and at Coalcomán.

Enyaliosaurus clarki (Bailey)

Ctenosaura clarki Bailey, Proc. U. S. Natl. Mus., 73:44, September 26, 1928. —Ovopeo (= Oropeo), Michoacán, México.

Enyaliosaurus clarki, Duellman and Duellman, Occ. Pap. Mus. Zool. Univ. Michigan, 598:1, February 16, 1959.

Twelve km. SSW of Apatzingán; Capirio (7); Cofradía (3); El Espinal (2); 32 km. E of Huetamo; Jazmin (5); Oropeo (10); Rancho Nuevo; Río Cancita, 12 km. E of Apatzingán (8); Tepalcatepec (3); Zicuiran (6).

This species is known only from the low areas of the Balsas-Tepalcatepec Basin between elevations of 200 and 510 meters. It is commonly found in the open arid tropical scrub forest dominated by *Prosopsis* sp., *Apoplanesia paniculata*, and *Cercidium plurifoliolatum*. Continued collecting in the Tepalcatepec Valley has borne out the suggestions of Duellman and Duellman (1959) concerning the distribution and abundance of this lizard. Also, continued collecting in Colima and on the Pacific coast has failed to reveal the presence of *Enyaliosaurus* there.

Phrynosoma asio Cope

Phrynosoma asio Cope, Proc. Acad. Nat. Sci. Philadelphia, 16:178, September 30, 1864.—Colima, Colima, México.

Apatzingán (4); San Salvador.

In Michoacán this species has been obtained only in the Tepalcatepec Valley and on the northern slopes of the Sierra de Coalcomán between 300 and 700 meters. Apparently the lizard is absent from the coastal lowlands of Michoacán and Guerrero. The distribution of this species, therefore, is discontinuous. One popu-

lation inhabits the lowlands of Colima and the Balsas-Tepalcatepec Basin inland to northern Guerrero and Morelos; a southern population inhabits the Plains of Tehuantepec in Oaxaca.

A juvenile from Apatzingán (USNM 47739) has a snout-vent length of 40.0 mm. and a tail length of 19.5 mm.

Sceloporus aeneus aeneus Wiegmann

Sceloporus aeneus Wiegmann, Isis von Oken, 21:370, 1828.—México. Type locality restricted to Tres Cumbres, Morelos, México, by Smith and Taylor (1950b:137).

Sceloporus aeneus aeneus, Smith, Occ. Pap. Mus. Zool. Univ. Michigan, 361:6, December 15, 1937.

Angahuan; Araparicuaro (2); Capácuaro (2); Carapan (11); Cherán (11); 18 km. WNW of Ciudad Hidalgo (10); Cuseño Station; Jeráhuaro; Los Conejos (36); Macho de Agua (7); Opopeo; Paracho (2); Pátzcuaro (4); Pino Gordo; 18 km. W of Quiroga (2); Tancítaro (49); Uruapan (14); 16 km. NW of Zacapu (5); between Zacapu and Zamora (2); 13 km. E of Zinapécuaro; 14 km. SE of Zitácuaro (14).

This small terrestrial species inhabits the pine and fir forests of the Cordillera Volcánica between elevations of 1850 and 3100 meters; apparently it is absent from the Sierra de Coalcomán. It seems to prefer rather open coniferous forests in which there is a more or less continuous cover of grasses on the ground. On warm sunny days the lizards can be observed scurrying about in the grass; in the early hours of the day, or on cold days, they are found beneath stones, logs, or dead clumps of bunch grass.

Sceloporus asper Boulenger

Sceloporus asper Boulenger, Proc. Zool. Soc. London, 1897:497, October, 1897.—La Cumbre de los Arrastrados, Jalisco, México.

Apatzingán (3); 10 km. E of Dos Aguas; Uruapan (41).

This strictly arboreal lizard is abundant in the mixed broad-leafed forest near Uruapan. The lizards are exceedingly wary and can be approached only with difficulty. In life males have pale blue bellies; the throat is pale pink. The pale gray dorsum marked with irregular darker gray blotches blends well with the color of the tree trunks on which the lizard lives. The one specimen from Dos Aguas was found on a pine tree; it provides the only record for the species from the Sierra de Coalcomán.

Sceloporus bulleri Boulenger

Sceloporus bulleri Boulenger, Proc. Zool. Soc. London, 1894:729, April, 1895.—Las Cumbre de los Arrastrados, Jalisco, México.

Acuaro de las Lleguas (13); Barolosa (9); Dos Aguas (61); 10 km. NE of Dos Aguas (5).

Heretofore this species has been known only from a few specimens from scattered localities in the Sierra Madre Occidental in

southwestern Jalisco and Sinaloa. The collection of a large series of these lizards in virgin pine forest at elevations of more than 2000 meters in the Sierra de Coalcomán now makes possible an analysis of variation in the species.

Superficially *S. bulleri* resembles *S. torquatus*, but *S. bulleri* is smaller, has more dorsal scales, fewer scales in the dark collar, and fewer femoral pores. In 88 specimens of *S. bulleri* there are 36-41 (38.7) dorsal scales and 2 or 3 (2.6) middorsal scales in the collar, as compared with 28-31 (29.3) dorsal scales and 3 or 4 (3.4) middorsal scales in the collar of 26 specimens of *S. torquatus* from Uruapan. In 20 adult males of *S. bulleri* there are 13-15 (14.3) femoral pores, and 13-16 (14.4) in 11 females; 13 males of *S. torquatus* have 14-21 (17.3) femoral pores, and 13 females have 15-21 (16.7). Seventeen adult males of *S. bulleri* have snout-vent lengths of 72-91 (82.0); ten females, 71-87 (75.7). In comparison, 13 adult males of *S. torquatus* have an average snout-vent length of 88.9 mm., and 13 females, 88.5 mm. In *S. bulleri* there is little variation in the head scales. The frontal is in contact with the interparietal in 63, and not in 24, specimens; the median frontonasal is in contact with the frontal in 13, and not in 74, specimens. In 39 specimens there are two canthals, and in 48 there is one; in 29 specimens there are three preauriculars, and in 58 there are four.

In life adult males have a pale blue tail, bright blue belly patches, a purplish blue throat, and pale blue lines on the sides of the head and neck.

This species was obtained at four localities in the high mountains of the Sierra de Coalcomán. In this mountain range *Sceloporus bulleri* apparently replaces *S. torquatus*, a species that is widespread in the Cordillera Volcánica and on the Mexican Plateau. At Dos Aguas and at Acuaro de las Lleguas the lizards were abundant in the tall pine forest, where they were found on standing pine trees, on pine logs, and on rock outcroppings.

Sceloporus dugesi intermedius Dugès

Sceloporus intermedius Dugès, La Naturaleza, 4:29, 1877.—La Noria, near Zamora, Michoacán, México.

Sceloporus dugesii intermedius, Smith, Univ. Kansas Sci. Bull., 24:663, February 16, 1938.

Cojumatlán (6); Jiquilpan (11); Lago de Camécuaro; Lago de Chapala; Morelia (23); Pátzcuaro (84); Quiroga (35); Sahuayo (4); Tacícuaro (2); Tangamandapio (17); Tangancícuaro (9); Zacapu (4); Zamora (11); Zinapécuaro (9).

This lizard is strictly an inhabitant of the Mexican Plateau, where it is found in rocky places, sometimes in pine-oak forest,

but more frequently in mesquite-grassland. It is a terrestrial species, and is most often seen on rock fences at elevations of 1500 to 2200 meters.

This species differs from *S. bulleri* and *S. torquatus* in having two rows of supraoculars, instead of one; also it has more dorsal scales. Twenty-six specimens of *Sceloporus dugesi intermedius* from Tangamandapio and Tangancícuaro have 44-48 (45.7) dorsal scales, as compared with an average of 38.7 in *S. bulleri* and 29.3 in *S. torquatus*. In life *Sceloporus dugesi intermedius* has a dull greenish gray dorsum; in males the belly patches are bright blue bordered medially by black, and the throat is bluish gray. The largest specimen examined is a male having a snout-vent length of 80 mm.

Sceloporus gadowae Boulenger

Sceloporus gadoviae Boulenger, Proc. Zool. Soc. London, 1905, 2:246, October 7, 1905.—Mezquititlán, Guerrero, México.

Chupio; El Sabino (77); La Playa (6); Río Marquez, 10 km. S of Lombardia (11).

Although this species has a rather extensive range in the Balsas-Tepalcatepec Basin in the state of Michoacán, Guerrero, Morelos, and Puebla, it is only locally abundant in that area. Usually these lizards are found on rocky cliffs in which there are many crevices for cover. *Sceloporus gadowae* is abundant on a conglomerate cliff along the Río Marquez south of Lombardia. Although the closely related *S. pyrocephalus* is abundant in the stream valley and in the hills above the cliff, *S. gadowae* has been found only on the cliff; few individuals of *S. pyrocephalus* have been observed on the cliff. A similar situation was discovered on a much more extensive conglomerate cliff along the Río Balsas near Mexcala, Guerrero. Near Tehuitzingo, Puebla, where *S. pyrocephalus* was not found, *S. gadowae* was found on conglomerate cliffs. Probably there is strong competition between the two species; possibly this has resulted in the restriction of *S. gadowae* to isolated cliff-habitats within the extensive range of the more widespread *S. pyrocephalus*.

In Michoacán *Sceloporus gadowae* has been found along the lower slopes of the Cordillera Volcánica at elevations from 250 to 1050 meters. All of the localities from which this lizard is known lie in the arid tropical scrub forest.

Sceloporus grammicus microlepidotus Wiegmann

Sceloporus microlepidotus Wiegmann, Herpetologia Mexicana, p. 51, 1834.—México. Type locality restricted to México, Distrito Federal, by Smith and Taylor (1950b:120).

Sceloporus grammicus microlepidotus, Smith and Laufe, Trans. Kansas Acad. Sci., 48:332, December, 1945.

Angahuari; Apo (10); Atzimba (3); Carapan (5); Cerro San Andrés (17); Cerro Tancítaro (18); Corupu; Cuseño Station (2); Jacona; Jeráhuaro (10); Macho de Agua; Mil Cumbres; 46 km. E of Morelia; 60 km. E of Morelia (2); Opopeo (14); Pátzcuaro (30); Puerto Hondo (19); San Gregorio (41); San José de la Cumbre (8); Sierra Patamba; Tancítaro (233); Tupátaro; Undameo; Uruapan (180); between Zacapu and Zamora; 24 km. SE of Zitácuaro; between Zurumbeneo and Cerro Garnica.

This small species of *Sceloporus* is an ubiquitous inhabitant of the coniferous forests from 1550 to 3100 meters in the Cordillera Volcánica. Usually it is seen on tree trunks, but occasionally on the ground. Near the lower limit of the altitudinal distribution of the species, as at Uruapan, individuals sometimes are found on broad-leafed trees. Apparently *Sceloporus heterolepis* replaces *S. grammicus microlepidotus* in the Sierra de Coalcomán.

Sceloporus heterolepis Boulenger

Sceloporus heterolepis Boulenger, Proc. Zool. Soc. London, 1894:731, April, 1895.—La Cumbre de los Arrastrados, Jalisco, México.

Araparicuaro; Cerro Barolosa (6); Dos Aguas (13); Los Conejos; 11 km. N of Uruapan (3).

Although Michoacán has not previously been included in the range of this lizard, it was first collected in the state by Gadow in 1908 (BMNH 1914.1.28.69 from Araparicuaro). The description of *S. heterolepis* given by Smith (1939:197) can be supplemented by data on the 23 specimens now in the collections of the Museum of Zoology at the University of Michigan. All have two canthals; there are 55 to 71 (63.6) scales in the middorsal row; 1 to 3 rows middorsally are somewhat enlarged and bordered on either side by a row of larger scales bearing high keels. There are 14 to 20 (16.2) femoral pores. Eight adult males have snout-vent lengths from 49 to 61 (58.0) mm. and tail lengths from 57 to 74 (66.0) mm.; four adult females have snout-vent lengths from 52 to 57 (55.2) mm. and tail lengths from 60 to 66 (63.5) mm. The smallest of eight juveniles has a snout-vent length of 28 mm. and a tail length of 32 mm. The dorsum in adults is pale grayish brown; there are three irregular chevron-shaped dark marks and a triangular dark brown mark above the insertion of the hind limbs; on the tail are dark brown rings. There are scattered faint blue flecks on the flanks and narrow transverse dark lines on the lower limbs. Males

have pale bluish green belly patches and an orange-salmon-colored throat; the belly in females is pale orange-tan. The juveniles have a more contrasting color pattern; the dark chevrons on the dorsum are bordered posteriorly by pale gray.

In Michoacán this species has been obtained in pine and pine-fir forests from 1800 to 2700 meters. On Cerro Barolosa and at Dos Aguas, both in the Sierra de Coalcomán, the lizards were found beneath the bark of dead, standing pines. In the Sierra de Coalcomán *Sceloporus heterolepis* seems to fill the niche of the small arboreal *Sceloporus* in the coniferous forest in southwestern México, a position held by *S. grammicus microlepidotus* in the Cordillera Volcánica; the latter species does not occur in the Sierra de Coalcomán. Five specimens of *Sceloporus heterolepis* are known from the Cordillera Volcánica, whereas 603 of *S. grammicus microlepidotus* have been collected there. The ecological relationships that exist between the two species in the Cordillera Volcánica are not known.

Insofar as is known, *Sceloporus heterolepis* reaches the southern limits of its range in the Sierra de Coalcomán and in the western part of the Cordillera Volcánica. Other records for the species are from the Sierra Madre Occidental in Jalisco. Langebartel (1959) described *Sceloporus shannonorum* from the mountains near the Durango-Sinaloa border; the single specimen of *S. shannonorum* differs significantly from *S. heterolepis* only in having fewer dorsal scales (48). The acquisition of additional material, especially from Nayarit and northern Jalisco, probably will provide a basis for showing that these two populations are conspecific.

Sceloporus horridus oligoporus Cope

Sceloporus oligoporus Cope, Proc. Acad. Nat. Sci. Philadelphia, 16:177, September 30, 1864.—Colima, Colima, México.

Sceloporus horridus oligoporus, Taylor, Univ. Kansas Sci. Bull., 24:520, February 16, 1938.

Aguililla; Apatzingán (50); Arteaga (2); Capirio (2); Cascada Tzararacua; Charapendo (4); Coahuayana (3); Coalcomán (32) 19 km. S of Corralito; 27 km. E of Dos Aguas; El Sabino (55); El Ticuiz; Huetamo (2); Jazmin; Jungapeo (2); La Orilla (2); La Placita; Limoncito (3); Playa Azul (5); Tzitzio (8); Uruapan (4); Volcán Jorullo (2); Ziracuaretiro; Zirimícuaro (13).

All of the specimens from Michoacán seem to be typical *S. horridus oligoporus;* none has more than six femoral pores.

Characteristically this species is found in open arid scrub forest; it reaches its greatest abundance in rocky areas in which there are scattered leguminous trees and bushes. It has been found in these

low trees and bushes almost as frequently as it has been found on the ground; none has been seen in large trees or far above the ground. Altitudinally, this species ranges from sea level to about 1600 meters.

Sceloporus melanorhinus calligaster Smith

Sceloporus melanorhinus calligaster Smith, Proc. U. S. Natl. Mus., 92:360, November 5, 1942.—Acapulco, Guerrero, México.

Aguililla; Apatzingán (18); Barranca de Herradero; Capirio (19); Coahuayana (4); Coalcomán (2); Cofradía (4); El Cerrito; El Sabino (33); El Ticuiz (3); La Placita (6); Lombardia (4); Playa Azul; Río Marquez, 10 km. S of Lombardia (2); Río Marquez, 13 km. SE of Nueva Italia (4); Salitre de Estopila; San Juan de Lima (2); Santa Ana; Tzitzio; Ziracuaretiro.

Smith (1942a:360) diagnosed *Sceloporus melanorhinus calligaster* as having fewer femoral pores than the other subspecies of *S. melanorhinus* and as having the lateral belly patches in the males confluent in the midline. Examination of forty specimens from the Tepalcatepec Valley and the coastal regions of Michoacán does not substantiate this diagnosis. The number of femoral pores varies from 15 to 22 (18.9); 14 individuals (35%) had 20 or more femoral pores. Smith (*loc. cit.*) stated that *S. melanorhinus* in Oaxaca had 18 to 27 (21.6) femoral pores and that 77 per cent of the specimens had more than 20 femoral pores. Of the 24 males examined from Michoacán, 18 have the lateral belly patches separated in the midline. Usually they are separated by no more than one scale, but in some individuals they are separated by two or more scales. Although the above data minimize certain differences between the northern and southern populations of this species, certain of the color pattern characters seem to be diagnostic of the subspecies inhabiting the Pacific lowlands from Guerrero to Nayarit. Large adults of *S. m. calligaster* have only a faint dorsal pattern, which in the subspecies *melanorhinus* and *stuarti* consists of a series of large, dark, interconnected triangles on the back. This pattern is present in young and small adults of *S. m. calligaster;* furthermore, in this subspecies the ventral coloration of the males differs from that found in the more southern populations. Adult males of *S. m. calligaster* have a black throat, that changes to brilliant blue posteriorly, and a large white spot medially on the chin. This spot is present in some specimens from Oaxaca and Chiapas, but, if present, it is much smaller and less distinct than in specimens from Michoacán. In *S. m. calligaster* the chest and midventral area are orange to salmon-color.

A male from Lombardia in life was colored as follows: Dorsum grayish tan bearing faint bluish gray flecks; chest deep salmon-

orange, this color continuing down midventral area to the somewhat paler groin; belly patches pale blue fading to pale green laterally; throat black anteriorly enclosing a white spot; throat blue posteriorly and bluish green posterolaterally.

Individual lizards were observed to change in dorsal color from a pale ashy gray to a rather dull brown. Normally, inactive individuals and those observed on overcast days were dull brown.

Sceloporus melanorhinus calligaster is found in trees in riparian situations in the lowlands to elevations of about 1500 meters. It does not inhabit the arid tropical scrub forest in the Tepalcatepec Valley or on the coast, but in those areas is found in the gallery forests along streams and rivers. The lizards are wary and live high in the trees; they are especially difficult to locate in the rainy season, when the trees are in full leaf.

Sceloporus pyrocephalus Cope

Sceloporus pyrocephalus Cope, Proc. Acad. Nat. Sci. Philadelphia, 16:177, September 30, 1864.—Colima, Colima, México.

Acahuato (2); Apatzingán (142); Arteaga (4); 26 km. S of Arteaga (4); Capirio (6); Chinapa; Chupio; 19 km. S of Corralito (5); El Sabino (220); Jazmin (3); La Placita (8); La Playa (14); La Salada (6); Lombardia (5); Nueva Italia (14); Ojos de Agua de San Telmo (2); Oropeo (3); Ostula; Punta de San Telmo (3); Río Cancita, 14 km. E of Apatzingán (13); Río Marquez, 10 km. S of Lombardia (10); Río Marquez, 13 km. SE of Nueva Italia (3); San Juan de Lima (2); Santa Ana (2); Tafetan (2); Tepalcatepec (2); Tzitzio (6); Volcán Jorullo (3).

This small species is extremely common in the Tepalcatepec Valley and noticeably less so on the coast. It is usually found on the ground in rocky areas, but males frequently have been seen on the trunks of low trees in the scrub forest. Altitudinally, it ranges from sea level to slightly more than 1000 meters. The sexes are readily distinguished in the field (Oliver, 1937; Smith, 1939; Duellman, 1954b). In the dry season only males were observed in the Tepalcatepec Valley, but in the rainy season both sexes were found in approximately the same numbers.

Sceloporus scalaris scalaris Wiegmann

Sceloporus scalaris Wiegmann, Isis von Oken, 21:370, 1828.—México. Type locality restricted to México, Distrito Federal, by Smith and Taylor (1950b:137).

Sceloporus scalaris scalaris, Smith, Occ. Pap. Mus. Zool. Univ. Michigan, 361:2, December 15, 1937.

Carapan (2); Cherán; Ciudad Hidalgo; Huingo (3); Jacona (3); Jiquilpan (2); Lago de Camécuaro (2); Lago de Chapala; Lago de Cuitzeo (5); Morelia (4); Pátzcuaro (4); Queréndaro; Quiroga; Tacícuaro (5); Tarécuaro; Zacapu (4); Zamora (4); Zinapécuaro (11).

This small terrestrial species does not seem to be abundant anywhere in the state. It sometimes is found in open pine, oak, or

pine-oak forest, but usually it is observed in areas supporting bunch grass. In such places the lizards sun and forage on the open ground and quickly take refuge in the large clumps of grass. Altitudinally, the species ranges from 1550 to 2300 meters. Although *Sceloporus scalaris scalaris* has been found in association with *S. dugesi intermedius, S. spinosus,* and *S. torquatus,* it does not seem to form any close ecological association with any of these species. In the pine forests of the Cordillera Volcánica *S. s. scalaris* is replaced by *Sceloporus aeneus aeneus,* another small terrestrial species that occurs in great abundance throughout the coniferous forests of the Cordillera Volcánica.

Sceloporus siniferus siniferus Cope

Sceloporus siniferus Cope, Proc. Amer. Philos. Soc., 11:159, 1869.—Pacific side of the Isthmus of Tehuantepec. Type locality restricted to Tehuantepec, Oaxaca, México, by Smith and Taylor (1950b:134).

Sceloporus siniferus siniferus, Smith and Taylor, Bull. U. S. Natl. Mus., 199:134, October 26, 1950.

Twenty-six km. S of Arteaga; Barranca de Bejuco (2); Coahuayana; El Ticuiz (2); La Mira; La Orilla (2); La Placita (9); Maruata; Ojos de Agua de San Telmo; Ostula (4); Playa Azul (6); Pómaro (2); Puerto de las Higuerita; Santa Ana (3).

This small terrestrial species inhabits the dense arid tropical scrub forest on the coast and lower foothills of the Sierra de Coalcomán to elevations of about 150 meters. It also occurs in the lower Balsas Valley, but it has not been found in the scrub forest of the broad Tepalcatepec Valley. Perhaps the large number of *Sceloporus siniferus* on the coastal lowlands is responsible for the small number there of *S. pyrocephalus,* another terrestrial species of about the same size. The latter is abundant in the Tepalcatepec Valley, where *S. siniferus siniferus* has not been found. *Sceloporus siniferus siniferus* is a fast runner and difficult to collect; consequently, the small number of specimens available is not indicative of its abundance.

Sceloporus spinosus spinosus Wiegmann

Sceloporus spinosus Wiegmann, Isis von Oken, 21:370, 1828.—México. Type locality restricted to Puebla, Puebla, México, by Smith and Taylor (1950b:116).

Sceloporus spinosus spinosus, Martín del Campo, Anal. Inst. Biol. México, 8:262, 1937.

Cojumatlán (2); Huetamo Road; Lago de Cuitzeo (4); Maravatio (8); Tupátaro (2).

Although this species is widespread on the southern part of the Mexican Plateau, it is uncommon in Michoacán. It has been col-

lected only in rather open situations in the mesquite-grassland on the plateau between 1500 and 2300 meters, where it has been found in association with *Sceloporus dugesi intermedius* and S. *scalaris scalaris*. Most specimens of *Sceloporus spinosus spinosus* have been observed on rock fences. In this habitat the species is the larger member of a pair of species, the smaller of which is *Sceloporus dugesi intermedius*.

Sceloporus torquatus torquatus Wiegmann

Sceloporus torquatus Wiegmann, Isis von Oken, 21:369, 1828.—México. Type locality restricted to México, Distrito Federal, by Smith and Taylor (1950b:126).

Sceloporus torquatus torquatus, Cope, Proc. Amer. Philos. Soc., 22:402, 1885.

Angahuan (31); Araparicuaro; Capácuaro (3); Carapan (11); Cerro Tancítaro; Cherán; Ciudad Hidalgo; Cojumatlán; Copándaro (2); Corupu (4); Cuseño Station (9); El Alamo; Jacona (6); Jiquilpan (2); Jungapeo (3); Lago de Camécuaro; Lago de Chapala; Lago de Cuitzeo (3); La Palma (2); Los Conejos (3); Los Reyes (3); Maravatio (9); Morelia (17); Paracho (3); Pátzcuaro (27); Pino Gordo; Queréndaro (2); Quiroga; Sahuayo (3); San José de la Cumbre; San Juan de Panangaricutiro; Tacícuaro (10); Tancítaro (200); Tangamandapio; Tangancícuaro (3); Temazcal (2); Tupátaro (5); Uruapan (136); Zacapu; Zinapécuaro (10); Zirimícuaro (12); Zitácuaro.

This large species inhabits the Mexican Plateau and the Cordillera Volcánica, but not the Sierra de Coalcomán, where apparently it is replaced by *Sceloporus bulleri*. *Sceloporus torquatus torquatus* usually is found in pine or pine-fir forests at elevations between 1450 and 3000 meters. In many places it is almost entirely arboreal, but in areas where there are many fallen trees or rock fences and rock piles, many individuals have been found on the ground near the rocks or logs. In the coniferous forests this species is associated with S. *grammicus microtepidotus* and S. *aeneus aeneus*.

The distinction made by Smith (1938:572) between the subspecies S. *torquatus torquatus* and *melanogaster* is slight. Individuals with pale bluish spots are found throughout the range of the species in Michoacán; spotting is especially evident in the young. Individuals having an incomplete nuchal collar have been found at Maravatio and at Zinapécuaro in the northern part of the state; in this character these specimens resemble S. *torquatus melanogaster*, which is found to the north from Guanajuato to Zacatecas and San Luis Potosí.

Sceloporus utiformis Cope

Sceloporus utiformis Cope, Proc. Acad. Nat. Sci. Philadelphia, 16:177, September 30, 1864.—Colima, Colima, México.

Nineteen km. S of Arteaga (2); Cascada Tzararacua (17); Coahuayana (3); Coalcomán (6); El Sabino (2); El Ticuiz (2); Ostula (3); Pómaro; Río Cachán; San Juan de Lima; Uruapan (26).

In Michoacán the range of this species is discontinuous. It has been found between 1050 and 1550 meters on the slopes of the Cordillera Volcánica, and on the coast and seaward slopes of the Sierra de Coalcomán up to an elevation of 900 meters. It is absent from the Tepalcatepec Valley. At Uruapan and at Cascada Tzararacua this lizard was found on the ground in oak forest or in open pine-oak forest; on the coast and foothills of the Sierra de Coalcomán it was found on the ground in the gallery forests along streams, and not in the scrub forest.

Urosaurus bicarinatus tuberculatus (Schmidt)

Uta tuberculata Schmidt, Amer. Mus. Novitates, 22:4, December 1, 1921.—Colima, Colima, México.

Urosaurus bicarinatus tuberculatus, Mittleman, Bull. Mus. Comp. Zool., 91:169, September, 1942.

Twenty-six km. S of Arteaga; Cascada Tzararacua (2); Chupio; Coahuayana; Coalcomán (8); El Sabino (2); Jungapeo; La Orilla (2); La Placita (4); Playa Azul (4); Pómaro (2); San Salvador (16); ? Tupátaro; Uruapan (12); Tzitzio; Zamora.

The known distribution and geographic variation of *Urosaurus bicarinatus* in southwestern México presents a confused picture. In general rugosity, specimens from the coastal region of Michoacán (Coahuayana, La Orilla, La Placita, Playa Azul, and Pómaro) resemble *U. bicarinatus tuberculatus* to the north along the Pacific coast. Furthermore, specimens from the coast have less stippling in the gular region than do those from the Sierra de Coalcomán and the slopes of the Cordillera Volcánica. Specimens from the mountains have greatly carinate enlarged dorsals, large lateral tubercles, and heavily stippled throats; in these characters they resemble specimens from Morelos, Guerrero, and Oaxaca. As mentioned by Peters (1954:14), some specimens from La Orilla and San Salvador are like *U. bicarinatus bicarinatus* in certain characters, and one specimen has the blue ventral patches restricted to the sternal area, a characteristic of *U. bicarinatus anonymorphus* of Oaxaca and eastern Guerrero. Examination of all available specimens from Michoacán indicates that the nature of the dorsal scales is of little value in separating the subspecies. The specimens from Michoacán are here provisionally referred to *U. bicarinatus tuber-*

culatus, because cursory examination of specimens from several localities between Nayarit and Oaxaca shows that there are only minor differences between the named populations. Individuals from the northern part of the range are more rugose and have larger blue ventral patches and less gular stippling than those from the south.

In Michoacán *Urosaurus bicarinatus tuberculatus* is found in wooded areas, not in open scrub forest, in the coastal area to elevations of about 900 meters, and along the slopes of the Cordillera Volcánica and the southern edge of the Mexican Plateau at elevations from 1000 to 1700 meters. The record for Tupátaro probably is erroneous, for no other specimens of this species are known from the central plateau. Essentially, the distribution of this species parallels that of *Sceloporus utiformis*, a strictly terrestrial species. *Urosaurus bicarinatus tuberculatus* lives on tree trunks. Below 1000 meters in the Tepalcatepec Valley *Urosaurus bicarinatus tuberculatus* is replaced by *Urosaurus gadowi*.

Urosaurus gadowi (Schmidt)

Uta gadovi Schmidt, Amer. Mus. Novitates, 22:3, December 1, 1921.—Cofradía, Jalisco, México (in error) = Cofradía, Michoacán, México (Duellman, 1958b:49).

Urosaurus gadovi, Mittleman, Bull. Mus. Comp. Zool., 91:154, September, 1942.

Acahuato (2); Apatzingán (56); 12-16 km. S of Apatzingán (12); Buenavista (7); Capirio (23); Cofradía (21); El Sabino (13); Guayabo; Jazmin; La Playa; La Salada (3); Nueva Italia (7); Rancho Nuevo; Río Cancita, 14 km. E of Apatzingán (5); Río Marquez, 10 km. S of Lombardia (2); Río Marquez, 13 km. SE of Nueva Italia (3); San Salvador (2); Santa Ana; Tepalcatepec; Volcán Jorullo (3); Zicuiran (2); Ziracuaretiro.

Although individuals of this species have been collected at elevations slightly exceeding 1200 meters on Volcán Jorullo and at 1100 meters at Ziracuaretiro on the southern slopes of the Cordillera Volcánica, for the most part these lizards are found at elevations of less than 800 meters, where they inhabit the open arid scrub forest of the Tepalcatepec Valley, a region to which this species is endemic (Duellman, 1958b:49). These small lizards usually are found on the trunks and main branches of the small trees in the scrub forest; in this habitat they are associated with *Sceloporus horridus oligoporus*, a much larger species.

Males have a pale orange spot on the throat and a pale blue belly; females have immaculate venters.

A specimen from Guayabo on the northern slopes of the Sierra de Coalcomán was referred to *Urosaurus irregularis* (Fischer) by Peters

(1954:15). I have studied this specimen (BMNH 1914.1.28.110), a female having a snout-vent length of 46 mm., and agree with Peters that it closely resembles Fischer's description and figure (1882: pl. 17, fig. 1). This specimen and those seen of *Urosaurus gadowi* all have pavementlike enlarged dorsal scales that are complete across the vertical line. In *U. gadowi* the enlarged dorsals usually are in four to six irregular rows; in the specimen from Guayabo the dorsals are in two rows. Although none of the other specimens of *U. gadowi* examined has only two rows of enlarged dorsals, I prefer to consider the specimen from Guayabo as an aberrant individual of that species, rather than *U. irregularis*. Guayabo is in the known range of *U. gadowi*. *Urosaurus irregularis* is known only from the type specimen in the Bremen Museum; the type locality, according to Fischer (1882:232), is "Aus dem Hochlande von Mexico." If an examination of the type specimen of *U. irregularis* shows it to be identical with *U. gadowi*, then *U. irregularis* would be the name for the lizards here referred to *U. gadowi*.

Mabuya brachypoda Taylor

Mabuya brachypoda Taylor, Univ. Kansas Sci. Bull., 38 (1):308, December 20, 1956.—Four kilometers east-southeast of Los Angeles de Tilarán, Guanacaste, Costa Rica.

El Sabino (42); La Placita; Playa Azul; Tzitzio (3).

Previously this species has been reported from La Placita as *Mabuya mabouya alliacea* by Peters (1954:15). Webb (1958:1311) provided evidence that Mexican specimens were conspecific with *Mabuya brachypoda*, as described from Costa Rica by Taylor (1956: 308). The large series in the Taylor collection studied by Webb and listed by him as being from Uruapan actually is part of a series collected by Hobart M. Smith at El Sabino at an elevation of 1050 meters, 30 kilometers south of Uruapan.

This species probably ranges throughout the coastal region of the state; individuals from La Placita and Playa Azul were taken in dense scrub forest near sea level.

Scincella assata taylori (Oliver)

Leiolopisma assatum taylori Oliver, Occ. Pap. Mus. Zool. Univ. Michigan, 360:12, November 20, 1937.—Santiago, Colima, México.

Scincella assata taylori, Mittleman, Herpetologica, 6:20, June 5, 1950.

Twenty-one km. S of Arteaga; Ostula.

The specimen from Ostula was obtained in semi-deciduous broadleaf forest at an elevation of 120 meters; that from 21 kilometers south of Arteaga was taken in oak forest at an elevation of 830 meters.

Both localities are on the coastal slopes of the Sierra de Coalcomán. Probably the species inhabits the heavy forests on the lower slopes of these mountains. The specimen from south of Arteaga (UMMZ 119117) in life had a tan dorsum and a bright orange-pink tail.

Eumeces altamirani Dugès

Eumeces altamirani Dugès, La Naturaleza, ser. 2, 1:485, 1891.—Apatzingán, Michoacán, México.

Twelve km. E of Apatzingán; El Sabino (4).

One specimen of this rare species was found beneath a rock in the open scrub forest 12 kilometers east of Apatzingán on July 3, 1955. Another skink, presumably of this species, was seen at Capirio. The specimen from east of Apatzingán is a male having a snout-vent length of 97 mm. and an incomplete tail. In most respects it compares favorably with accounts of the species given by Taylor (1936b:55 and 1936c:102). The frontal is divided by a transverse suture; the enlarged dorsal scales are arranged in 11 pairs anteriorly, followed by 48 unpaired enlarged scales. The head and middorsal area are brown; there is a pale tan stripe on the edges of the vertebral and paravertebral rows, bordered by a dark brown stripe on the paravertebral row, which, in turn, is bordered by a pale tan stripe on the lateral edge of the paravertebral scale row and the median edge of the adjacent scale row. The stripes extend from the neck to the base of the tail. The flanks are mottled with brown and cream-color; the labials are cream-color barred by brown; the venter is a pale cream-color.

Dugès (1891:485) described *Eumeces altamirani* from "las regiones cálidas del Estado de Michoacán" and subsequently (1896: 480) gave Apatzingán as a locality for the species. Presumably he had only one specimen. In 1935 Hobart M. Smith collected the species at El Sabino on the lower slopes of the Cordillera Volcánica bordering the Tepalcatepec Valley. All of the known specimens are from this valley and the adjacent slopes, an area to which the species apparently is endemic.

Eumeces colimensis Taylor

Eumeces colimensis Taylor, Publ. Field Mus. Nat. Hist., zool. ser., 20:77, May 15, 1935.—Colima, Colima, México.

Coalcomán; Salitre de Estopila.

The species was reported by Peters (1954:16); no additional material has been discovered. The species is known only from foothills and low mountains at elevations between 130 and 950 meters in Michoacán and Colima.

Eumeces copei Taylor

Eumeces copei Taylor, Proc. Biol. Soc. Washington, 46:133, June 5, 1933.—10 miles southeast of Asunción, México, México. Cerro Tancítaro (3); Zacapu.

This member of the *Eumeces brevirostris*-group has been found only in pine or pine-fir forests at elevations from 1800 to 2700 meters. It probably ranges throughout the high mountains of the state north of the Tepalcatepec Valley; its apparent absence in other parts of the Cordillera Volcánica, other than on Cerro Tancítaro, is surprising. The species has been taken near Asunción in the state of México and at Lagunas de Zempoala in Morelos.

In this species the lateral pale yellow stripe, which is bordered below by dark brown, extends to the groin and onto the base of the tail. The dorsolateral stripe is separated from the copper-colored middorsum by a narrow brown stripe.

Eumeces dugesi Thominot

Eumeces Dugesii Thominot, Bull. Soc. Philom. Paris, ser. 7, 7:138, 1883.—Guanajuato. Type locality restricted to Guanajuato, Guanajuato, México, by Smith and Taylor (1950b:169).

Carapan (6); Cherán (5); Opopeo (2); 17 km. S of Pátzcuaro (3); San José de la Cumbre (2); Tancítaro (2); Tangancícuaro; Uruapan; Zacapu.

Individuals of this species frequently have been found beneath rocks and logs in pine-oak, pine, or fir forests from elevations of 1550 to 1850 meters. To judge from specimens available, *E. dugesi* probably is the most abundant and widespread species of skink in the state.

In this species the lateral yellow stripe is indistinct and is persistent only in the axilla; the dorsolateral stripes terminate anterior to the hind limbs and are not separated from the tan dorsum.

Eumeces indubitus Taylor

Eumeces indubitus Taylor, Univ. Kansas Sci. Bull., 21:257, November 27, 1934.—Near Cuernavaca, Morelos, México.

Puerto Hondo.

The one specimen of this species from Michoacán was collected by Edward H. Taylor in pine forest at Puerto Hondo, near Zitácuaro, at an elevation of about 2750 meters (Taylor, 1935:466). The species is known from the high mountains of eastern Michoacán, western México, and northern Morelos.

Eumeces parvulus Taylor

Eumeces parvulus Taylor, Proc. Biol. Soc. Washington, 46:175, October 26, 1933.—Tepic, Nayarit, México.

El Ticuiz; La Placita; Pómaro (2); San Pedro Naranjestila (3).

Aside from the specimens reported by Peters (1954:17), one other specimen was obtained at El Ticuiz. It has 22 scale rows, 3 supraoculars in contact with the frontal, 2 postlabials, and a unicolored olive-tan dorsum. In life the anterior dorsolateral stripes were pale pinkish tan, the labials cream color, the throat white, and the tail pale blue. All specimens were found in semi-deciduous broadleaf forest at elevations of less than 500 meters on the seaward slopes of the Sierra de Coalcomán.

Ameiva undulata sinistra Smith and Laufe

Ameiva undulata sinistra Smith and Laufe, Univ. Kansas Sci. Bull., 31 (1):59, May 1, 1946.—Manzanillo, Colima, México.

Apatzingán (9); 19 km. S of Arteaga (3); Barranca de Bejuco (2); Coahuayana (6); Coalcomán (3); El Ticuiz (10); La Placita (2); Limoncito (3); Ostula (2); Playa Azul; Salitre de Estopila; San Juan de Lima (2); San Pedro Naranjestila (4).

Six males and six females from the Tepalcatepec Valley have more femoral pores than do 16 males and nine females from the coastal lowlands; the ranges and average number of femoral pores in the former are 40-50 (44.8) for males and 38-40 (38.6) for females; males from the coast have 34-44 (39.2), and females have 32-40 (36.2) femoral pores. In all specimens the number of lamellae beneath the fourth toe varies from 26 to 33 (29.7). In life juveniles have a pale olive-tan dorsum and a dorsolateral dark band, superimposed on which is a row of darker brown spots. The dorsolateral band is bordered below by a narrow cream-colored stripe. The tail is tan above and grayish white below; the belly is pale bluish white. Adult males are brilliantly colored in life. A male having a snout-vent length of 108 mm. had a rusty brown dorsum and bright blue bars on the flanks separated by dark brown interspaces. The side of the head was pale green, and the chin and throat were golden yellow. In some specimens the throat is orange. Juveniles and subadults have dark flecks on the brown or tan middorsal area, but these are absent in the largest males.

This species inhabits the heavily wooded areas in the lowlands to elevations of about 950 meters. In the Tepalcatepec Valley it has been found only in gallery forests along streams. In both the Tepalcatepec Valley and the coastal lowlands there is a noticeable absence of large adults in the dry season.

Cnemidophorus calidipes Duellman

Cnemidophorus calidipes Duellman, Occ. Pap. Mus. Zool. Univ. Michigan, 574:1, December 23, 1955.—Capirio, Michoacán, México.

Apatzingán (56); 12-20 km. S of Apatzingán (5); 19 km. E of Apatzingán (5); 25 km. S of Arteaga; Capirio (57); El Espinal (13); Jazmin (9); 11 km. S of Lombardia; Nueva Italia.

This small, distinctive species of the *sexlineatus*-group of *Cnemidophorus* was discovered in the Tepalcatepec Valley in 1955 (Duellman, 1955); subsequent field studies showed it to be widespread in the valley (Duellman, 1960c). One specimen (KU 29747) is from the relatively arid, low Pacific slope of the Sierra de Coalcomán, 25 kilometers south of Arteaga. All other specimens have been taken at elevations of 200 to 650 meters in the Tepalcatepec Valley, where the species characteristically inhabits the open scrub forests of the valley floor, especially the *Cercidium-Prosopis-Apoplanesia* associations, where there is a sparse growth of grasses. In this habitat it is most frequently seen in association with *Cnemidophorus costatus zweifeli* and *C. deppei infernalis*.

Aside from the charaters given in Table 5, *Cnemidophorus calidipes* differs from other species of *Cnemidophorus* in Michoacán by possessing a complete (or nearly so) supraorbital semicircle-series of granules; in other species the granules seldom extend anteriorly beyond the posterior border of the frontal.

Cnemidophorus communis communis Cope

Cnemidophorus communis Cope, Proc. Amer. Philos. Soc., 17:95, 1877.—No type locality given; type locality restricted to Colima, Colima, México, by Zweifel (1959a:74).

Cnemidophorus communis communis, Zweifel, Bull. Amer. Mus. Nat. Hist., 117:74, April 27, 1959.

Aguililla (2); Apatzingán (6); 13 km. S of Arteaga (2); 19 km. S of Arteaga (3); Capirio (3); Coahuayana (3); Coalcomán (44); El Ticuiz; between El Ticuiz and Ojos de Agua de San Telmo; La Placita (6); Pómaro (2); Río Cachán; Salitre de Estopila; San Juan de Lima.

The specimens from Coalcomán and the coastal localities were referred to *Cnemidophorus sacki copei* by Peters (1954:18) and Duellman (1954b:12). Zweifel (1959a) referred these specimens to *Cnemidophorus communis communis* and pointed out the probable sympatry of *C. communis* and *C. costatus* (= *sacki* of Zweifel) in the Tepalcatepec Valley.

There is considerable geographic variation in the number of dorsal granules around the midbody. Sixteen specimens from the coastal regions of Michoacán have 129-146 (136.3) granules; nine from the Tepalcatepec Valley have 124-137 (128.3), and 44 from Coalcomán at an elevation of 950 meters in the Sierra de Coalcomán, intermedi-

TABLE 5.—COMPARISON OF THE TEN SPECIES AND SUBSPECIES OF CNEMIDOPHORUS IN MICHOACÁN (SCALE COUNTS ARE FOR SPECIMENS FROM MICHOACÁN ONLY)

SPECIES	Dorsal granules	Femoral pores	Adult color pattern	Throat color	Maximum snout-vent length
calidipes	66–86 (75)	31–47 (39)	Light brown dorsum with vertical blue bars and spots	Pink	79 mm.
communis communis	105–146 (124)	38–52 (44)	Green dorsum with six rows of yellow spots	Pink	135 mm.
costatus occidentalis	97–102 (99)	37–43 (39)	Cross-bars anteriorly and pale spots posteriorly	Pink	126 mm.
costatus zweifeli	91–117 (106)	32–49 (41)	Lateral and dorsolateral rows of spots; paravertebrals fused with pale green middorsum	Pink with blue spot	132 mm.
deppei deppei	116–117 (116)	37–38 (37)	Green paravertebral and dorsolateral stripes; lateral stripe broken into row of bluish spots	Black	93 mm.
deppei infernalis	91–120 (101)	31–43 (36)	Green paravertebral and dorsolateral stripes; broad cream lateral stripe; reddish flanks	Black	84 mm.
lineatissimus exoristus	108–140 (122)	32–47 (39)	Paravertebral stripes fused with yellow middorsal stripe; vertical bars on flanks	Pink and black	98 mm.
lineatissimus lineatissimus	117–126 (121)	32–37 (35)	Eight distinct stripes plus partially fused vertebrals	Bluish-pink and black	96 mm.
lineatissimus lividus	126–164 (148)	32–48 (38)	Broad middorsal stripe; paravertebrals distinct; blue lateral spots	Pink and black	106 mm.
scalaris	80–92 (86)	32–41 (35)	Six distinct cream stripes; tan spots in dark fields	Orange-pink	95 mm.

ate geographically between the coast and the Tepalcatepec Valley, have 105-144 (119.7). The number of granules in specimens from the coast of Michoacán compares favorably with the range of 118-154 (137.8) for 34 specimens from Colima, Colima (Zweifel, 1959a:107). Aside from the characters given in Table 5, *C. communis communis* can be distinguished from other members of the *Cnemidophorus sexlineatus*-group (*calidipes, costatus,* and *scarlaris*) by its relatively small post-antebrachial scales.

Although this is the largest species of *Cnemidophorus* in Michoacán (adult males attain a snout-vent length of 135 mm.), it is neither widespread nor abundant. On the coastal lowlands it occurs primarily with *Cnemidophorus lineatissimus lividus.* In the coastal lowlands there is little open scrub forest, a type of habitat that seems to be preferred by *C. communis communis.* In the Tepalcatepec Valley, *C. communis communis* occurs in the open scrub forest with the more abundant large species *C. costatus* (subspecies *zweifeli*). Only in the scrub forest in the Coalcomán Valley, where no other species of *Cnemidophorus* occurs, is *C. communis communis* abundant.

Cnemidophorus costatus occidentalis Gadow

Cnemidophorus communis occidentalis Gadow, Proc. Zool. Soc. London, 1906, 1:339, August 23, 1906.—Type locality restricted to Ixtlán, Nayarit, México, by Smith and Taylor (1950b:182).

Cnemidophorus costatus occidentalis, Zweifel, Copeia, No. 1:98; March 17, 1961.

Jiquilpan (4).

Only four specimens from the extreme northwestern part of the state are referable to this subspecies. These have 97 to 102 dorsal granules at midbody and lack the blue gular band or spot characteristic of the subspecies in the Tepalcatepec Valley. Probably *C. costatus occidentalis* ranges throughout the Chapala depression, but to the east it is replaced by *Cnemidophorus scalaris scalaris.*

Cnemidophorus costatus zweifeli Duellman

Cnemidophorus sacki zweifeli Duellman, Univ. Kansas Publ. Mus. Nat. Hist., 10:589, May 2, 1960.—Capirio, Michoacán, México.

Apatzingán (107); Buenavista (3); Capirio (31); Charapendo (12); Chinapa (2); 19 km. S of Corralito (3); Jazmin (2); between La Playa and Volcán Jorullo (2); Limoncito (3); 14 km. S of Lombardia (11); Nueva Italia (15); Río Marquez, 10 km. S of Lombardia (2); Río Marquez, 13 km. SE of Nueva Italia; Tafetan (18); 14 km. E of Tepalcatepec (2); Tzitzio (11); 19 km. S of Tzitzio; Volcán Jorullo (5); Ziracuaretiro; Zirimícuaro.

These lizards were referred to *Cnemidophorus sacki copei* by Duellman (1954b:12 and 1955:6); Duellman (1960a) described the subspecies *zweifeli* and assigned it to *Cnemidophorus sacki.* Zwei-

fel (1961:98) used the specific name *C. costatus* for the whiptails on the southwestern part of the Mexican Plateau (*C. c. occidentalis*). Since *occidentalis* and *zweifeli* are conspecific, the combination *C. costatus zweifeli* is used here for the population inhabiting the Tepalcatepec Valley.

This lizard is abundant in the Tepalcatepec Valley, where it lives in open and dense scrub forest, usually at elevations of less than 1000 meters. Throughout the valley it is found in association with *Cnemidophorus deppei infernalis,* and in the lower parts of the valley it also is associated with *Cnemidophorus calidipes.* Observations made in the dry season indicate that large adults are not active at that time.

On the coastal lowlands and in the valleys in the Sierra de Coalcomán *Cnemidophorus costatus zweifeli* is replaced by *C. communis communis.* To the east in the Balsas Basin *C. costatus zweifeli* intergrades with *C. costatus costatus.*

Cnemidophorus deppei deppei Wiegmann

Cnemidophorus deppei Wiegmann, Herpetologia Mexicana, p. 29, 1834.—México. Type locality restricted to Tehuantepec, Oaxaca, México, by Smith and Taylor (1950b:179).

Cnemidophorus deppei deppei, Cope, Trans. Amer. Philos. Soc., 17:31, 1892.

Salitre de Estopila; San Pedro Naranjestila.

This small species, which is extremely abundant on the coastal lowlands of Guerrero, seems to be rare on the coast of Michoacán, where it has been taken at elevations of 130 and 500 meters in open situations in otherwise forested areas. Duellman and Wellman (1960:25) discussed these specimens in relation to their subspecific assignment. They were referred to *Cnemidophorus deppei lineatissimus* by Peters (1954:18).

Cnemidophorus deppei infernalis Duellman and Wellman

Cnemidophorus deppei infernalis Duellman and Wellman, Misc. Publ. Mus. Zool. Univ. Michigan, 111:32, February 10, 1960.—Mexcala, Guerrero, México.

Acahuato; Apatzingán (227); Capirio (3); El Sabino; Jazmin; La Playa (6); Lombardia (6); Nueva Italia (4); Río Marquez, 10 km. S of Lombardia (6); Río Marquez, 13 km. SE of Nueva Italia (10); south of Tancítaro; Volcán Jorullo (3).

This is one of the most abundant and widespread lizards in the Tepalcatepec Valley. Throughout its range it is ecologically associated with *Cnemidophorus costatus zweifeli,* which ranges to elevations somewhat higher than the 1050 meters known for *C. deppei infernalis.* This small lizard reaches its greatest abundance

in grassy areas on the floor of the Tepalcatepec Valley, where in the *Cercidium-Prosopis-Apoplanesia* associations it occurs with *Cnemidophorus calidipes.*

Duellman and Wellman (1960) discussed the variation and relationships of *Cnemidophorus deppei,* of which the subspecies *infernalis* is restricted to the Balsas-Tepalcatepec Basin.

Cnemidophorus lineatissimus exoristus Duellman and Wellman

Cnemidophorus lineatissimus exoristus Duellman and Wellman, Misc. Publ. Mus. Zool. Univ. Michigan, 111:44, February 10, 1960.—Rancho Santa Ana, four kilometers northeast of San Salvador, Michoacán, México.

Thirteen to 25 km. S of Arteaga (18); Capirio (19); Limoncito (13); Santa Ana (22).

As in *Cnemidophorus calidipes,* the distribution of this subspecies seems to be restricted to the Tepalcatepec Valley, except in the vicinity of Arteaga, where it occurs on the southern slope of the Sierra de Coalcomán. As pointed out by Duellman and Wellman (1960:46), the specimens from south of Arteaga are like those from the Tepalcatepec Valley in scutellation and coloration, and not like *Cnemidophorus lineatissimus lividus* from the geographically closer coastal lowlands.

In the Tepalcatepec Valley *Cnemidophorus lineatissimus exoristus* inhabits gallery forests along the larger streams; in this habitat it is associated with *Ameiva undulata sinistra.* From the other species of *Cnemidophorus* in Michoacán, *C. lineatissimus exoristus* can be distinguished by the possession of seven longitudinal stripes in adults and by the characters of scutellation given in Table 5.

Cnemidophorus lineatissimus lineatissimus Cope

Cnemidophorus lineatissimus Cope, Proc. Amer. Philos. Soc., 17:94, 1877.—Colima and Guadalajara. Type locality restricted to Colima, Colima, México, by Smith and Taylor (1950b:179).

Cnemidophorus lineatissimus lineatissimus, Duellman and Wellman, Misc. Publ. Mus. Zool. Univ. Michigan, 111:41, February 10, 1960.

Boca de Apiza (4).

These specimens have 117 to 126 dorsal granules at midbody, a noticeably lower count than that for *Cnemidophorus lineatissimus lividus* on the coast of Michoacán, which has 126 to 164 (148). Apparently these specimens represent immature *C. lineatissimus lineatissimus;* the differences between these and *C. lineatissimus lividus* from nearby localities indicate that possibly the populations are distinct species and not subspecies, as suggested by Duellman and Wellman (1960:41).

Cnemidophorus lineatissimus lividus Duellman and Wellman

Cnemidophorus lineatissimus lividus Duellman and Wellman, Misc. Publ. Mus. Zool. Univ. Michigan, 111:50, February 10, 1960.—Maruata, Michoacán, México.

Barranca de Bejuco (4); Boca de Apiza (2); Coahuayana (6); El Ticuiz (7); La Placita (11); Maruata (7); Motín del Oro; Ostula (5); Playa Azul (4); Playa Cuilala (2); Pómaro (2); Salitre de Estcpila (2); San Pedro Naranjestila.

This is the most abundant and widespread species of *Cnemidophorus* on the coastal lowlands of Michoacán, where it ranges from sea level to elevations of about 500 meters. In this area it inhabits dense arid scrub forest and semi-deciduous broad-leafed forest. Both of these habitats are continuous, or nearly so, along the lowlands and foothills of the Sierra de Coalcomán. This in itself may explain the abundance of *Cnemidophorus lineatissimus* and the relative scarcity of *C. deppei* and *C. communis* in the coastal area, for *C. deppei* and *C. communis* usually inhabit more open arid scrub forest, as occurs in the Tepalcatepec Valley. Living in the dense scrub forest with *C. lineatissimus* is *Ameiva undulata sinistra.*

Cnemidophorus scalaris Cope

Cnemidophorus gularis scalaris Cope, Trans. Amer. Philos. Soc., 17:47, 1892.—Chihuahua, Chihuahua, México.

Cnemidophorus scalaris, Zweifel, Bull. American Mus. Nat. Hist., 117:72, 1959.

Araro (2); Jacona; Lago de Cuitzeo (42); Morelia; 21 km. N of Morelia (4).

Zweifel (1959a:72) assigned the small species of *Cnemidophorus* having a relatively low number of dorsal granules and inhabiting the southern part of the Mexican Plateau to *C. scalaris,* which he diagnosed as rarely exceeding 100 mm. in snout-vent length and always having an average of less than 100 dorsal granules at mid-body and usually less than 90. Forty-two specimens from the south shore of Lago de Cuitzeo (UMMZ 119558) have 80-91 (85.8) dorsal granules. Four specimens from 21 kilometers north of Norelia (UIMNH 6952 and UMMZ 104743) have 89, 78, 92, and 84 granules; one from Morelia (UMMZ 104742) has 78; two from Araro (UMMZ 119522) have 80 and 87; one from Jacona (UIMNH 24703) has 88.

Since no large adult males are present in the series from Michoacán, an adequate comparison of coloration between these and populations on the northern part of the Mexican Plateau cannot be made. *Cnemidophorus scalaris* is a name applied to the lizards inhabiting the Mexican Plateau from Chihuahua south to Puebla by Zweifel (1959a:72). It is doubtful if all of the popula-

tions assigned to this subspecies belong there; possibly more than one species is involved, but the paucity of material prevents further analysis at this time.

Heloderma horridum horridum (Wiegmann)

Trachyderma horridum Wiegmann, Isis von Oken, 22:421, 1829.—México. Type locality restricted to Huajintlán, Guerrero, México, by Smith and Taylor (1950b:193).

Heloderma horridum horridum, Bogert and Martín del Campo, Bull. Amer. Mus. Nat. Hist., 109:20, April 16, 1956.

Apatzingán; Coalcomán; La Placita; Oropeo; Parácuaro.

This species is known from elevations of less than 1000 meters in the Tepalcatepec Valley, the Sierra de Coalcomán, and the coastal lowlands. Specimens from Coalcomán, La Placita, and Parácuaro came from areas of dense woods; those from Apatzingán and Oropeo might have come from patches of dense woods in the otherwise open scrub forest of the Tepalcatepec Valley.

Gerrhonotus imbricatus imbricatus Wiegmann

Gerrhonotus imbricatus Wiegmann, Isis von Oken, 21:379, 1828.—México. Type locality restricted to México, Distrito Federal, by Smith and Taylor (1950b:201).

Gerrhonotus imbricatus imbricatus, Dunn, Proc. Acad. Nat. Sci. Philadelphia, 88:475, October 20, 1936.

Acuaro de las Lleguas (9); Cerro Barolosa (4); Cerro Tancítaro (36); Dos Aguas (22); Paracho; Sierra Patamba; Tinguidín; Zacapu.

Specimens from the Sierra de Coalcomán are noticeably different from those inhabiting the mountains rising from the Mexican Plateau. Of 45 specimens from Cerro Tancítaro and adjacent areas on the Mexican Plateau and in the Cordillera Volcánica, 15 have twelve longitudinal rows of dorsal scales and 30 have fourteen rows. Of seven specimens from the state of México, 5 have twelve rows and 2 have fourteen; of nine specimens from central Veracruz, 8 have twelve rows and one has fourteen; of six specimens from Hidalgo, 5 have twelve rows and one has sixteen; of two specimens from Guanajuata, one has fourteen and the other has sixteen rows. All of the 35 specimens from the Sierra de Coalcomán have sixteen rows. Furthermore, these specimens have the superciliary row extended anteriorly, so that the anterior superciliary is in broad contact with the loreal. Specimens from Cerro Tancítaro have a shorter superciliary row, so that the anterior superciliary is not in broad contact with the loreal. These characters were used by Tihen (1949:220) to distinguish *Gerrhonotus imbricatus ciliaris* from *G. imbricatus imbricatus.* According to Tihen, the subspecies *G. imbricatus*

ciliaris ranges from Guanajuato and Hidalgo northward to Chihuahua and Coahuila, whereas the nominal subspecies occurs from Michoacán and Hidalgo southward to Oaxaca. Specimens from the Sierra de Autlán in Jalisco are like those from Cerro Tancítaro; consequently, there seems to be no connection between the populations of *G. imbricatus ciliaris* in the mountains of the northern part of the Mexican Plateau with the *ciliaris*-like individuals found in the Sierra de Coalcomán. The acquisition and study of additional material from throughout the range of the species is necessary to clarify the picture of geographic variation. Until then, I prefer to consider all of the specimens from Michoacán as *Gerrhonotus imbricatus imbricatus.*

The largest specimen is a male having a snout-vent length of 136 mm. Two juveniles collected in July 24, 1960, have snout-vent lengths of 36 and 42 mm. A specimen having a snout-vent length of 127 mm. and a tail length of 145 mm. was regurgitated by a *Crotalus pusillus,* which had a body length of 550 mm.

Gerrhonotus imbricatus imbricatus is an inhabitant of coniferous forests. In the Cordillera Volcánica it occurs from 1500 to 3500 meters at the top of Cerro Tancítaro. In the Sierra de Coalcomán it occurs from 2100 to 2700 meters. On July 4, 1955, a pair was found in copulation beneath a pine log at 2700 meters on Cerro Barolosa. The male was lying on top of the female and was holding her head firmly in his jaws; the male's tail was curled under the female's tail, so that the cloacae were in contact.

Serpentes

Typhlops braminus (Daudin)

Eryx braminus Daudin, Hist. . . . des reptiles, 7:279, 1803.—Vazagapatam, India.

Typhlops braminus, Cuvier, Règne animal, ed. 2, 2:73, 1829.

Apatzingán; Arteaga.

Both specimens known from Michoacán were collected by Gadow in 1908. Peters (1954:20) remarked that the specimen from Arteaga probably does not indicate a rapid spreading of the species, which most likely was introduced into México at the time that vessels were stopping at Acapulco from the Philippines (Taylor, 1940b:444), but instead may indicate that pack trains from Acapulco passed through the Sierra de Coalcomán. The occurrence of this snake along a long-used *camino* substantiates this belief.

Leptotyphlops bressoni Taylor

Leptotyphlops bressoni Taylor, Copeia, No. 1:5, March 9, 1939.—Hacienda El Sabino, Michoacán, México.

El Sabino.

This species still is known definitely only from the type specimen collected on the lower slopes of the Cordillera Volcánica at the northern edge of the Tepalcatepec Valley. A specimen (now lost) reported from Aguililla by Cope (1887:63) possibly represents this species (see Smith and Taylor, 1945:21, and Peters, 1954:20).

Leptotyphlops gadowi Duellman

Leptotyphlops gadowi Duellman, Copeia, No. 2:93, May 29, 1956.—Apatzingán, Michoacán, México.

Apatzingán.

No additional specimens of this species have been collected since the species was described by Duellman (1956b:93). Data given with the specimen by Gadow indicate that it came from his camp above Apatzingán at an elevation of about 800 meters. Although the exact position of this camp is unknown, the lower slopes of the Cordillera Volcánica above Apatzingán usually support arid scrub forest at elevations below 1000 meters. Therefore, this species probably is an inhabitant of the arid scrub forest.

Leptotyphlops phenops bakewelli Oliver

Leptotyphlops bakewelli Oliver, Occ. Pap. Mus. Zool. Univ. Michigan, 360:16, November 20, 1937.—Paso del Río, Colima, México.

Leptotyphlops phenops bakewelli, Smith, Proc. U. S. Natl. Mus., 93:445, October 29, 1943.

La Placita (4); La Salada; Ostula.

The five specimens from the coastal lowlands are from elevations of less than 150 meters; these were collected by Peters (1954:20); the specimen from La Salada is from an elevation of 580 meters in the Tepalcatepec Valley. Peters (*loc. cit.*) remarked that the rostral and the tip of the tail that were described as white by Oliver (1937: 17) actually are sulphur-yellow in life.

Loxocemus bicolor Cope

Loxocemus bicolor Cope, Proc. Acad. Nat. Sci. Philadelphia, 13:77, June 30, 1861.—La Unión, El Salvador.

Loxocemus sumichrasti Bocourt, Ann. Sci. Nat., ser. 6, 4:1, 1876.—Tehuantepec, Oaxaca, México.

Apatzingán (6); La Orilla; Lombardia.

As noted by Peters (1954:21), this species was not recorded from Michoacán by Smith and Taylor (1945:27), but Gadow (1930:30) collected a specimen at La Orilla in 1908. This specimen (BMNH

1914.1.28.124) is a male having 235 ventrals and 47 caudals, a dark brown dorsum, and cream-colored labials and venter. The anterior chin-shields are considerably longer than the scales bordering the chin-shields. In these characters this specimen agrees with the diagnosis of *Loxocemus bicolor* given by Taylor (1940c:447), who revived *Loxocemus sumichrasti* Bocourt. Of the six specimens from Apatzingán in the Tepalcatepec Valley, three males have 243 to 253 (246.6) ventrals and 44 to 45 (44.3) caudals; three females have 238 to 247 (244.0) ventrals and 42 to 44 (43.0) caudals. Certain characters of scutellation utilized by Taylor for separating *L. bicolor* and *L. sumichrasti* are inconsistent in this series. The chin-shields are longer than the adjacent scales, like those illustrated in *L. bicolor* by Taylor (*op. cit.*, fig. 1). The relative lengths of the prefrontal and internasal sutures are subequal, or the prefrontal suture is slightly longer. Thus, in these characters of scutellation these snakes are like *L. bicolor*, but in coloration they are like *L. sumichrasti;* the dorsal color in life was an iridescent dark bluish gray, and the belly was pale gray or bluish gray.

The supposed differences in scutellation between *L. bicolor* and *L. sumichrasti* have been questioned by Woodbury and Woodbury (1944:360); these authors treated *L. sumichrasti* as a subspecies of *L. bicolor.* As pointed out by Zweifel (1959b:5), such an arrangement is not tenable, for, although individuals with each kind of color pattern have not been collected together at any one locality, the over-all geographic picture is one of sympatric distribution. Only snakes having the coloration of *L. sumichrasti* have been collected in the Balsas-Tepalcatepec Basin. I agree with Zweifel (*loc. cit.*) that on the basis of morphological similarities and sympatric distribution, *L. bicolor* and *L. sumichrasti* seem to be dimorphic phases of the same species, showing no more striking differences in coloration than *Lampropeltis getulus californiae,* a now classical example of pattern dimorphism in snakes.

In Michoacán, as in other parts of its range, *Loxocemus bicolor* inhabits arid scrub forest environments at low elevations.

Boa constrictor imperator Daudin

Boa imperator Daudin, Hist. nat. . . . des reptiles, 5:150, 1803.—México. Type locality restricted to Córdoba, Veracruz, México, by Smith and Taylor (1950a:347).

Boa constrictor imperator, Forcart, Herpetologica, 7:199, December 31, 1951.

Apatzingán (4); Coalcomán; El Sabino (2); La Placita; La Playa (2); Lombardia; Nueva Italia (2); Río Cachán; Rio Marquez, 13 km. SE of Nueva Italia; Río Nexpa; Volcán Jorullo.

These specimens have come from a variety of habitats from elevations of less than 1,000 meters. The species seems to be equally

abundant in the broad-leafed semi-deciduous forests of the coastal foothills and in the arid Tepalcatepec Valley. In the latter area most of the specimens were collected at night.

Coniophanes fissidens dispersus Smith

Coniophanes fissidens dispersus Smith, Proc. U. S. Natl. Mus., 91:106, November 13, 1941.—El Limoncito, Guerrero, México.

Arteaga.

Further collecting in southern Michoacán has failed to add additional material of this species, which is known in the state from the one specimen collected by Gadow in 1908. The species possibly ranges throughout the coastal foothills of the Sierra de Coalcomán. Peters (1954:21) described the specimen from Arteaga.

Coniophanes lateritius lateritius Cope

Coniophanes lateritius Cope, Proc. Acad. Nat. Sci. Philadelphia, 13:524, March 31, 1862.—Guadalajara, Jalisco, México.

Coniophanes lateritius lateritius, Smith and Grant, Herpetologica, 14:20, April 25, 1958.

Nineteen km. S of Arteaga.

The one specimen available from Michoacán of this apparently rare species was discussed by Wellman (1959:127), who pointed out that although the specimen was geographically intermediate between the subspecies *C. l. lateritius* (Jalisco and Nayarit) and *C. l. melanocephalus* (Morelos and Puebla), the specimen (UMMZ 118954) was like *C. l. lateritius* in scutellation and in color pattern differed from other known specimens of the species in having had in life a pale orange, instead of a brick-red, dorsum. Additional specimens from the Sierra de Coalcomán will be required in order to determine whether this specimen is a representative of an orange-colored population or merely is aberrant in coloration.

The present specimen is from an elevation of 900 meters in oak forest on the southern slopes of the Sierra de Coalcomán; other locality records for the species indicate that it inhabits broad-leafed forest in foothills from Nayarit to Puebla.

Conophis vittatus vittatus Peters

Conophis vittatus Peters, Monats. Akad. Wiss. Berlin, p. 519, 1860.—No type locality given. Type locality restricted to Laguna Coyuca, Guerrero, México, by Smith and Taylor (1950a:331).

Conophis vittatus vittatus, Smith, Jour. Washington Acad. Sci., 31:119, March 17, 1941.

Arteaga; Coalcomán (4); La Playa; 19 km. S of Tzitzio.

All specimens of this terrestrial snake have been collected in areas of scrub forest between 800 and 1100 meters above sea level. Since

the species is known from the coastal regions of Guerrero and Colima, its absence from the cost of Michoacán is unexplainable; probably the lack of specimens from these areas is due solely to inadequate collecting.

Conopsis biserialis Taylor and Smith

Conopsis biserialis Taylor and Smith, Univ. Kansas Sci. Bull., 28 (2):333, November 12, 1942.—Ten miles west of Villa Victoria, México, México.

Capácuaro (5); Cerro San Andrés; Cherán; Ciudad Hidalgo; Macho de Agua (4); Pátzcuaro (8); Tancítaro (24); Uruapan (9); 24 km. SE of Zitácuaro (14).

This species is abundant in the coniferous forests at elevations from 1550 to 2800 meters throughout the Cordillera Volcánica; apparently it does not occur in the Sierra de Coalcomán.

On August 1, 1956, a copulating pair was found beneath a rock at Capácuaro.

One of the best characters to distinguish this species from *Toluca lineata,* which occurs with *Conopsis* throughout its range in Michoacán, is the presence of large, black ventral blotches in *Conopsis biserialis,* as contrasted with the two rows of small black spots in *Toluca lineata.*

Conopsis nasus Günther

Conopsis nasus Günther, Catalogue . . . snakes . . . British Museum, p. 6, 1858.—California (in error). Type locality restricted to Guanajuato, Guanajuato, México, by Smith and Taylor (1950a:330).

Carapan (2); Erongaricuaro; Maravatio (3); Morelia (2); Nahuatzén; Pátzcuaro (7); Tacícuaro (8); Tancítaro.

This species has been collected in oak, pine-oak, and fir forests at elevations of 1900 to 2450 meters on the mountains rising from the Mexican Plateau. It does not seem to be so abundant as *Conopsis biserialis.* Sufficient ecological data to determine differences in habitat between the two species have not been compiled.

Diadophis dugesi Villada

Diadophis punctatus dougesii Villada, La Naturaleza, 3:226, 1875.—Potreros de Balbuena, Distrito Federal, México.

Diadophis dugesii, Blanchard, Bull. Chicago Acad. Sci., 7:51, December 30, 1942.

Morelia (2); Pátzcuaro; Quiroga.

Apparently this snake is uncommon in Michoacán. It has been found only at elevations of 1900 to 2200 meters in pine and pine-oak forests on the mountains rising from the Mexican Plateau.

Dryadophis melanolomus stuarti Smith

Dryadophis melanolomus stuarti Smith, Proc. U. S. Natl. Mus., 93:418, October 29, 1943.—Acapulco, Guerrero, México.

Coahuayana; El Ticuiz; La Placita (3); Punto San Juan de Lima; Punto San Telmo.

The few specimens indicate that in Michoacán, as elsewhere on the Pacific coast of México, this species is restricted to forested regions on the coastal plain. It does not occur in the Tepalcatepec Valley.

The coloration, in life, of a juvenile (UMMZ 114604) is as follows: The dorsum is uniform pale grayish tan on posterior one-third of body and on tail; anteriorly there are pale grayish tan middorsal blotches separated by grayish white interspaces, which are about one-half the length of the blotches. Posteriorly the blotches are less distinct, fading into the uniform grayish tan ground color of the posterior part of the body. The blotches extend laterally onto the fourth and fifth scale rows. Large squarish lateral intercalary blotches of darker brown interconnect with the dorsal blotches. The top of the head is pale olive-brown; a dark brown postorbital stripe extends from the eye to the posterior edge of the last upper labial. The labials, chin, and ventrals 1-30 are creamy white, changing to a dusty cream-color posteriorly; the chin and ventrals 1-30 are heavily spotted with dark brown. The iris is a cream-color above and chocolate brown below; the tongue is blue.

Drymarchon corais rubidus Smith

Drymarchon corais rubidus Smith, Jour. Washington Acad. Sci., 31:474, November 11, 1941.—Rosario, Sinaloa, México.

Apatzingán (5); Arroyo El Salto; Arteaga; Capirio; El Sabino (7); La Palma; La Placita; Ostula; San Juan de Lima.

Not all of the specimens from Michoacán are typical in color pattern of this subspecies, as defined by Smith (1941a:475). All specimens from the Tepalcatepec Valley are uniformly black above; they have reddish or cream-colored chins and the anterior two-thirds of the belly salmon-pink or reddish buff. Individuals from the Sierra de Coalcomán (Arteaga and Arroyo El Salto) are like those from the Tepalcatepec Valley. Three specimens from the coastal lowlands differ noticeably in color pattern:

UMMZ 104504, adult male (Ostula).—Pale brown above flecked with black anteriorly; at midbody, flecks form narrow transverse bands that become progressively wider posteriorly, until on tail no brown pigment evident, all ventrals reddish buff, except last eight, which are black.

UMMZ 104602, adult female (La Placita).—Black above, reddish cross-bands and flecks on all of body; dorsal and ventral surfaces of tail black; chin cream-color and entire belly reddish buff.

UMMZ 114626, adult male (San Juan de Lima).—Black above; dull rust-colored cross-bands on anterior half of body; chin white; belly rust-colored on anterior two-thirds of body and black posteriorly.

One specimen from La Palma on the Mexican Plateau (KU 29275) has the top of the head an olive-color, the entire dorsum black, the chin and ventrals 1-42 a cream-color, remainder of venter black, and all of the labials heavily barred with black. A juvenile from Capirio in the Tepalcatepec Valley (UMMZ 114627) is black above and has pale olive-colored flecks on the anterior one-third of the body; the top of the head is dark olive-brown, and the sides of the head are somewhat paler. Anteriorly the belly is a cream-color; posteriorly it is black.

The specimens from the Tepalcatepec Valley are typical of *Drymarchon corais rubidus*. Those from the coastal lowlands differ in having large areas of brown or red pigment on the dorsum, a condition not mentioned by Smith in his description of the subspecies. The specimen from La Palma, like many others from various localities on the Mexican Plateau, resembles in certain characters *D. corais orizabensis* (Smith, *op. cit.*:477). Our knowledge of the geographical variation in coloration in this species is incomplete; many populations have been assigned to subspecific rank without justification.

In Michoacán this species is found from sea level to 1350 meters in the Sierra de Coalcomán and to 1300 meters at La Palma on Lago de Chapala. It has been collected in scrub forest, semi-deciduous broad-leafed forest, and oak forest.

Drymobius margaritiferus fistulosus Smith

Drymobius margaritiferus fistulosus Smith, Proc. U. S. Natl. Mus., 92:383, November 5, 1942.—Miramar, Nayarit, México.

Apatzingán (3); Coahuayana; Coalcomán (3); El Sabino (3); El Ticuiz; 12 km. S of Tzitzio.

This snake is abundant in the lowlands of the state; the few specimens listed above are indicative not of the rarity, but rather of the speed and agility, of this diurnal snake. It most frequently is found near water, where there is a dense growth of vegetation. One individual was observed in a large pool inhabited by several small *Rana pipiens*, and another was seen along the bank of a hyacinth-choked

river channel. A third individual was captured while it was in pursuit of a *Cnemidophorus*.

This species has been collected on the coastal lowlands and seaward foothills of the Sierra de Coalcomán and in the Tepalcatepec Valley to elevations of 1150 meters.

Elaphe triaspis intermedia (Boettger)

Pityophis intermedius Boettger, Ber. Offen. Vereins. Naturk., 22:148, 1883. —México. Type locality restricted to Hacienda El Sabino, Michoacán, México, by Dowling (1960:74).

Elaphe triaspis intermedia, Mertens and Dowling, Senckenbergiana, 33:201, November 15, 1952.

Twenty-four km. E of Apatzingán; Chupio; El Sabino (4); 11 km. E of Emiliano Zapata.

Dowling (1960) has shown that specimens from the Balsas-Tepalcatepec Basin have fewer ventrals and caudals than those from the Sierra del Sur or the coast. All specimens from Michoacán were collected in open forest, either scrub or oak forest. They were found in drier situations than those described for the species in southern Tamaulipas by Martin (1958:69). In Michoacán *Elaphe triaspis intermedia* is known from the Tepalcatepec Valley, the lower slopes of the Cordillera Volcánica, and the western edge of the Mexican Plateau at an elevation of 1350 meters. It probably occurs in the lower parts of the Sierra de Coalcomán and along the Pacific coast, for it is known from the coastal lowlands of Guerrero and Colima. In August, 1951, I saw a snake that probably was this species in Barranca de Bejuco.

Enulius unicolor (Fischer)

Geophis unicolor Fischer, Abh. Nat. Ver. Bremen, 7:227, 1882.—México. Type locality restricted to Chilpancingo, Guerrero, México, by Smith and Taylor (1950a:331).

Enulius unicolor, Taylor and Smith, Univ. Kansas Sci. Bull., 25:247, July 10, 1939.

Between Ario de Rosales and La Playa; Coalcomán; Jungapeo (4); between Zitácuaro and Tuxpan.

This small snake has been collected from beneath rocks in brushy areas and broad-leafed forest between 900 and 1800 meters; it has not been found in coniferous forest. The limited ecological data suggest that the species inhabits the transition zone between the tropical scrub forest and the temperate hardwood forest.

All of the specimens have 17 rows of scales; four males have 169-178 (174.2) ventrals and 102-111 (106.8) caudals; two females have 192 and 195 ventrals and 96 and 87 caudals. Three individuals have one postocular on one side and two on the other; in the other

specimens there are two postoculars on each side. The largest male has a body length of 232 mm. and a tail length of 130 mm.; the largest female has a body length of 274 mm. and a tail length of 119 mm.

Geagras redimitus Cope

Geagras redimitus Cope, Jour. Acad. Nat. Sci. Philadelphia, ser. 2, 8:141, 1876.

San Juan de Lima (2).

Previously this species was known definitely only from the Plains of Tehuantepec, Oaxaca. *Sphenocalamus lineolatus* was described by Fischer (1883:5) from Mazatlán; this name has been placed in the synonymy of *Geagras redimitus* Cope. Although Fischer gave the type locality only as "Mazatlán" and did not designate the state, it is probable that the type originated from Mazatlán, Sinaloa. The present specimens are from a locality almost midway between Tehuantepec and Mazatlán and support the possibility that *Geagras* ranges along the Pacific coast of México from Oaxaca to Sinaloa.

The two specimens from Michoacán (UMMZ 114446-7), both males, have 118 and 122 ventrals, 31 and 33 caudals, body lengths of 108 and 81 mm., and tail lengths of 20 and 15 mm. Both have 1-1 preoculars, 1-1 postoculars, 1-2 temporals, 6-6 upper labials, and 5-5 lower labials. In life, the dorsum was pale tan; the top of the head and the middorsal and lateral stripes were dark brown; the belly was white. The occipital spots were pale pinkish tan. Both specimens were found beneath rocks in tropical semi-deciduous forest at an elevation of 15 meters on the coastal plain.

Geophis dugesi Bocourt

Geophis dugesii Bocourt, Miss. Scientifique au Mexique et dans l'Amerique Centrale, Rept., livr. 9:573, 1883.—Tangancícuaro, Michoacán, México.

Carapan; Tangancícuaro; Zacapu.

Aside from the three specimens listed above, there are two (SU 4407-8) bearing the data "Michoacán." Bocourt (1883:574) stated that the type specimen from Tangancícuaro had six or seven pale cross-bands on the anterior part of the body. An illustration, presumably of the same specimen, by Dugès (1884:Pl. 9) shows five distinct and one indistinct cross-bands. Of the four specimens that I have examined, none has more than three pale cross-bands, and one has only one indistinct cross-band. Two females have 154 and 158 ventrals and 38 and 37 caudals; two males have 150 and 151 ventrals and 43 and 42 caudals.

This species is known only from elevations between 1750 and 2050

meters on the southwestern edge of the Mexican Plateau in the state of Michoacán.

Geophis incomptus Duellman

Geophis incomptus Duellman, Occ. Pap. Mus. Zool. Univ. Michigan, 605:3, May 29, 1959.—Dos Aguas, Michoacán, México.

Dos Aguas (15).

This species, which seems to be related to *Geophis maculiferus*, is known only from the pine-oak forest in the vicinity of Dos Aguas (elevation 2100 meters) in the Sierra de Coalcomán. Aside from the five specimens comprising the type series, there are ten other specimens in the Museum of Zoology at the University of Michigan collected by Floyd L. Downs in July, 1960. Data from these specimens and those comprising the type series show that in this sample seven males have 146-153 (149.3) ventrals and 35-37 (36.0) caudals; eight females have 150-154 (152.4) ventrals and 29-34 (32.5) caudals. The largest specimen is a female with a body length of 344 mm. and a tail length of 53 mm.

Geophis maculiferus Taylor

Geophis maculiferus Taylor, Univ. Kansas Sci. Bull., 27:119, December 30, 1941.—Near Cicio [*sic*] = Tzitzio, Michoacán, México.

Tzitzio.

The type and only known specimen of *Geophis maculiferus* (UIMNH 25078) is a female having 140 ventrals and 30 caudals, dorsal scales in 15 rows, one postocular, and an anterior temporal. Only one other species in México has dorsal scales in 15 rows and has an anterior temporal; that species is *G. incomptus*, which differs from *G. maculiferus* in having six or seven lower labials, instead of five, and in having the edges of the ventrals dark, instead of a uniformly cream-colored belly.

The locality from which the specimen was obtained lies at an elevation of 1630 meters on the southern slope of the Cordillera Volcánica. At that elevation there is an interdigitation of arid tropical scrub forest and pine-oak forest; probably *Geophis maculiferus* inhabits the pine-oak forest.

Geophis nigrocinctus Duellman

Geophis nigrocinctus Duellman, Occ. Pap. Mus. Zool. Univ. Michigan, 605:1, May 29, 1959.—Dos Aguas, Michoacán, México.

Dos Aguas (3).

The three specimens comprising the type series of the species were found beneath logs and in a stump in pine-oak forest at an elevation of 2100 meters. A discussion of the variation in these

specimens and of probable relationships of the species was given by Duellman (1959). Floyd Downs spent several days at Dos Aguas in July, 1960; although he found ten specimens of *Geophis incomptus,* no further specimens of *G. nigrocinctus* were obtained.

Geophis petersi Boulenger

Geophis petersii Boulenger, Catalogue Snakes . . . British Museum, 2:321, September 23, 1894.—Mexico City. Type locality restricted to Pátzcuaro, Michoacán, México, by Smith and Taylor (1950a:335).

Cheran; Coalcomán; Morelia; Pátzcuaro (6).

This seems to be the most widespread species of *Geophis* in Michoacán. It has been found at elevations between 950 and 2350 meters, chiefly in pine or pine-oak forest. Boulenger (1894:321) described *Geophis petersi* from a specimen stated to be from Mexico City, a locality which probably is in error. The only localities from which the species is definitely known are those listed in this account.

Three males and five females from the Mexican Plateau and the Cordillera Volcánica have respectively 140-144 (141.7) and 143-151 (146.0) ventrals and 39-41 (40.0) and 29-35 (33.2) caudals. All have dorsal scales in 15 rows, 1 postocular, no anterior temporal, and a relatively small triangular supraocular. The specimen from Coalcomán (UMMZ 104698) was referred to *Geophis nasalis* by Peters (1954:22). This specimen is abnormal in several characters; in five places there is a fusion and separation of the vertebral and paravertebral scale rows, producing a change from 17 to 15 rows of dorsal scales. Fusion of the three rows takes place at the level of the 8th, 41st, 47th, 54th, and 65th ventrals. Furthermore, there is a small secondary postocular on each side of the head. In other characters the specimen is like *G. petersi;* the resemblances to that species are greater than to *G. nasalis,* which has been recorded from Guatemala and southern Chiapas.

Geophis tarascae Hartweg

Geophis tarascae Hartweg, Occ. Pap. Mus. Zool. Univ. Michigan, 601:1, May 4, 1959.—Uruapan, Michoacán, México.

Uruapan (3).

A female of this species was collected in the Parque Nacional at the north edge of Uruapan in 1899, and a male was taken there in 1947; these specimens were used by Hartweg in his description of the species. Floyd L. Downs obtained another specimen in the Parque Nacional on July 19, 1960. It has 164 ventrals and 46 caudals; in life, the ground color of the neck was brown with a purplish tint; the dorsal markings were black; the chin was a cream-

color, and the belly was white. This specimen is distinguished from those of all other species of *Geophis* in Michoacán in that it has dark irregular cross-bars on the dorsum and a row of dark spots on the venter.

Hypsiglena torquata ochrorhyncha Cope

Hypsiglena ochrorhyncha Cope, Proc. Acad. Nat. Sci. Philadelphia, 12:246, November 15, 1860.—Cape San Lucas, Baja California, México.

Hypsiglena torquata ochrorhyncha, Bogert and Oliver, Bull. Amer. Mus. Nat. Hist., 83:378, March 30, 1945.

Tupátaro.

The systematic status of the geographic variants of *Hypsiglena* in México and southwestern United States has been commented on by several authors. Tanner (1944) considered *H. torquata* and *H. ochrorhyncha* to be distinct species; Bogert and Oliver (1945:379) and Duellman (1957b:238) presented evidence indicating that *H. torquata* and *H. ochrorhyncha* intergrade in Sinaloa and southern Sonora. In *Hypsiglena* the scutellation, including the numbers of labials, dorsals, ventrals, and caudals, seem to vary in a clinal manner. Nevertheless, these snakes can be divided into two distinct populations on the basis of the nuchal color pattern, consisting of an *ochrorhyncha*-type (a broad dark nape-band, the lateral edges of which extend anteriorly and fuse with a postorbital stripe, and a narrow nape stripe extending from the posteromedian edges of the parietals to the dark nape band) and a *torquata*-type (a somewhat narrower dark nape-band bordered anteriorly by a pale nuchal area, and no dark nape stripe). Snakes having the *ochrorhyncha*-type of nuchal pattern are found on the Mexican Plateau from Michoacán northward into the desert regions of Sonora and the southwestern United States. Snakes having the *torquata*-type of pattern are found on the coastal lowlands and adjacent slopes of the Sierra Madre Occidental from southern Sinaloa to Colima and thence inland in the Balsas-Tepalcatepec Basin to Morelos and Guerrero. An exception is *Hypsiglena torquata dunklei* from Forlón and San Fernando, Tamaulipas; it has the *torquata*-type of nuchal pattern. The distributional picture is somewhat complicated because some individuals having the *torquata*-type of nuchal pattern also have a faint nape stripe. If these are taken as exceptions, the general picture of distribution in México is *H. t. torquata* on the Pacific lowlands from Sinaloa southward to the Balsas Basin and *H. t. ochrorhyncha* on the Mexican Plateau.

Smith (1943:433) resurrected *Hypsiglena jani* Dugès for the snakes of the *ochrorhyncha*-type on the southern part of the Mexican

Plateau. He stated that the southern specimens differed from northern ones in having a nuchal spot 9 or 10 scales in length, as compared with a spot 2 to 6 scales in length in northern specimens. A cursory examination of specimens from the areas between Arizona and Michoacán showed that there is a gradual increase in the size of the spot from north to south. If no other characters can be found to distinguish the populations, they should be considered as a single subspecies.

Hypsiglena affinis differs from *H. torquata* in possessing 19 instead of 21 rows of dorsal scales. Additional material is needed from the western slopes of Jalisco and the Barrancas in Zacatecas and Durango, before definite allocation of *affinis* can be made.

Bogert and Oliver (1945:379) discussed the status of certain named populations in Baja California and concluded that only one species occurs there, and that the species probably is conspecific with *H. torquata.* A careful review of the genus *Hypsiglena* might show that there is only one species.

The one specimen from Michoacán (USNM 46513) is from an elevation of about 2300 meters near the southern edge of the Mexican Plateau.

Hypsiglena torquata torquata (Günther)

Leptodeira torquata Günther, Ann. Mag. Nat. Hist., ser. 3, 5:170.—Laguna Island, Nicaragua (in error).

Hypsiglena torquata torquata, Taylor, Univ. Kansas Sci. Bull., 25:371, July 10, 1939.

Apatzingán; Capirio; Cofradía.

Specimens from the three mentioned localities have the dark nuchal spot bordered anteriorly by a pale blotch. In life the specimen from Capirio (UMMZ 114424) had rich reddish brown dorsal spots; the dorsal ground color was grayish white above and somewhat more gray laterally. The pale nuchal area was a cream-color, and the iris was grayish red.

All of the specimens were found in the arid scrub forest in the Tepalcatepec Valley at elevations between 200 and 350 meters.

Imantodes gemmistratus gracillimus (Günther)

Dipsas gracillima Günther, Biol. Centrali-Americana, Rept., p. 177, July, 1895.—southern México. Type locality restricted to Acapulco, Guerrero, México, by Smith and Taylor (1950a:331).

Imantodes gemmistratus gracillimus, Zweifel, Amer. Mus. Novitates, 1961:12, September 16, 1959.

La Orilla.

The specimen from La Orilla was reported by Peters (1954:23) as *Imantodes gemmistratus oliveri;* Zweifel (1959c) showed that *I. g.*

oliveri did not range west of Tehuantepec and that the snakes inhabiting the coastal lowlands of Guerrero, Michoacán, and Colima were assignable to the subspecies *gracillimus*. It may be assumed that this subspecies ranges throughout the coastal lowlands and foothills of the Sierra de Coalcomán.

Imantodes gemmistratus latistratus (Cope)

Dipsas gemmistrata latistrata Cope, Bull. U. S. Natl. Mus., 32: 68, 1887.—Southern Jalisco. Type locality restricted to Guadalajara, Jalisco, México, by Smith and Taylor (1950a:334).

Imantodes gemmistratus latistratus, Zweifel, Amer. Mus. Novitates, 1961:3, September 16, 1959.

El Sabino.

The one specimen from Michoacán was collected near the upper limits of the scrub forest on the slopes of the Cordillera Volcánica. Zweifel (1959c:10) stated that in certain aspects of coloration this specimen was like *I. gemmistratus gracillimus*, but in scutellation and other features of coloration it was like *I. g. latistratus*. There are too few specimens of this species to define the ranges of the various subspecies with any degree of accuracy, but from the limited number of specimens available, it seems that *I. gemmistratus gracillimus* occurs on the Pacific lowlands from Guerrero northward to Colima. Northward on the Pacific lowlands from Colima to Sinaloa and in the Balsas-Tepalcatepec Basin is found *I. gemmistratus latistratus*.

Lampropeltis doliata (Linnaeus)

Coluber doliatus Linnaeus, Systema naturae, ed. 12, 1:379, 1766.—Charleston, South Carolina.

Lampropeltis doliata, Klauber, Copeia, No. 1:11, April 15, 1948.

Coalcomán (3); El Sabino; 24 km. W of Morelia; Río Nexpa; Uruapan.

The few specimens of this species from Michoacán show a wide range of variation; furthermore, the present systematic status of the subspecies of *Lampropeltis doliata* portrays an incongruous pattern of distribution. Specimens from the Sierra de Coalcomán have relatively narrow red bands that are not interrupted dorsally by extensions of the black rings; the scales in the red bands have black tips. The specimen from El Sabino (EHT-HMS 5253) and the one from the Río Nexpa on the coast (USNM 31491) have broader red bands; the scales in the red bands do not have black tips. A specimen from 24 kilometers west of Morelia (UIMNH 17782) and one from Uruapan (UMMZ 121508) have the red bands interrupted dorsally by extensions from the black rings.

Specimens from the Sierra de Coalcomán were referred to *L. doliata blanchardi* by Peters (1954:24), who noted that in some

characters these snakes were like *L. d. nelsoni* and in others like *L. d. polyzona.* The individual from El Sabino was referred to *L. d. nelsoni* by Taylor (1940c:465); the one from 24 kilometers west of Morelia was referred to *L. d. arcifera* by Smith (1942c:198). If these assignments are correct, three subspecies of *Lampropeltis doliata* occur in Michoacán: *blanchardi* in the Sierra de Coalcomán, *nelsoni* on the coast and in the Tepalcatepec Valley, and *arcifera* on the Mexican Plateau and in the Cordillera Volcánica. Such a distribution is plausible, but the few specimens and our general lack of knowledge of the variation and relationships of the different populations do not permit a definite assignment at this time.

Lampropeltis ruthveni Blanchard

Lampropeltis ruthveni Blanchard, Occ. Pap. Mus. Zool. Univ. Michigan, 81:8, April 28, 1920.—Pátzcuaro, Michoacán, México.

Morelia; Pátzcuaro; Tacícuaro.

At the present time this species is known definitely from only three localities on the Mexican Plateau in Michoacán. An incomplete skin from El Sabino (EHT-HMS 5438) was referred to this species by Taylor (1940c:465); the specimen cannot be found, so verification of the identification cannot be made at this time.

Leptodeira latifasciata (Günther)

Hypsiglena latifasciata Günther, Biologia Centrali-Americana, Reptilia, p. 138, October, 1894.—Southern México. Type locality restricted to Huajintlán, Morelos, México, by Smith and Taylor (1950a:331).

Leptodeira latifasciata, Dunn, Proc. Natl. Acad. Sci., 22:696, December, 1936.

Apatzingán; El Sabino; La Playa; 32 km. E of Nueva Italia.

This nocturnal snake apparently ranges throughout the arid Balsas-Tepalcatepec Valley to elevations of about 1050 meters. It has been collected only in the arid scrub forest. Aside from the specimens listed by Duellman (1958a:93), there is one (UMMZ 120223) having eight body blotches, a body length of 510 mm. and a tail length of 103 mm.

Leptodeira maculata (Hallowell)

Megalops maculatus Hallowell, Proc. Acad. Nat. Sci. Philadelphia, 13:488, March 31, 1862.—"Tahiti." Type locality restricted to Manzanillo, Colima, México, by Duellman (1958a:54).

Leptodeira maculata, Duellman, Bull. Amer. Mus. Nat. Hist., 114:53, February 24, 1958.

Aguililla (2); Apatzingán (24); Arteaga (2); Capirio (3); Charapendo (2); Coahuayana (3); Cofradía; Cuatro Caminos; La Placita (3); Lombardia (69); Nueva Italia (29); Pómaro; Río Marquez, 10 km. S of Lombardia (2); Salitre de Estopila; Tafetan (2); Volcán Jorullo.

This snake is abundant in the arid Tepalcatepec Valley; most of the specimens have been collected in arid scrub forest at elevations of less than 500 meters. With the onset of the rains in late June and early July, large numbers of these snakes can be found around temporary pools, where they feed on small frogs and toads. In the dry season few individuals were found, and all of those were beneath cover. Specimens from the coast have more body-blotches than do those from the Tepalcatepec Valley (Duellman, 1958a:56); otherwise the snakes show little variation.

Leptodeira splendida bressoni Taylor

Leptodeira bressoni Taylor, Univ. Kansas Sci. Bull., 25:321, July 10, 1939.—Hacienda El Sabino, Michoacán, México.

Leptodeira splendida bressoni, Duellman, Bull. Amer. Mus. Nat. Hist., 114:84, February 24, 1958.

Coalcomán (3); El Sabino (3); Uruapan (5).

The range of *Leptodeira splendida bressoni* apparently does not overlap that of *Leptodeira maculata;* the latter is restricted to the lower reaches of the arid scrub forest, whereas *L. s. bressoni* inhabits the upper limits of the arid scrub forest and the lower part of the pine-oak forest. Specimens have been collected between 950 and 1630 meters on the slopes of the Cordillera Volcánica and at 950 meters in the Sierra de Coalcomán. At Uruapan individuals were found beneath rocks along a stream and in a stone fence. *Leptodeira duellmani,* which was described from Coalcomán by Peters (1954:25), is an aberrant individual of *L. s. bressoni* (Duellman, 1958a:56).

Leptophis diplotropis (Günther)

Ahaetulla diplotropis Günther, Ann. Mag. Nat. Hist., ser. 4, 9:25, 1872.—Tehuantepec, Oaxaca, México.

Leptophis diplotropis, Bocourt, Mission scientifique au Mexique et dans l'Amerique Centrale, Reptiles, livr. 15:835, 1897.

Between Aguililla and Dos Aguas; Arteaga; Coalcomán; El Diezmo; El Sabino (5); La Playa; Ocorla.

Most specimens of this species have been collected in tropical semi-deciduous forest at elevations of less than 1000 meters. In the Sierra de Coalcomán one was taken in pine-oak forest at an elevation of 1700 meters near Ocorla; another was found in broad-leafed forest between Aguililla and Dos Aguas at an elevation of 1600 meters. Most individuals have been seen in trees or bushes. The absence of broad-leafed forest in the Tepalcatepec Valley probably accounts for the absence of this snake in that area.

Manolepis putnami (Jan)

Dromicus putnami Jan, Elenco sistematico degli Ofidi, p. 67, 1863.—San Blas, Nayarit, México.

Manolepsis putnami, Smith and Taylor, Bull. U. S. Natl. Mus., 187:92, October 5, 1945.

La Placita (3); Maquili; Ostula.

In Michoacán the species has been found only in tropical semideciduous forest on the lower slopes of the Sierra de Coalcomán. From the observations made by Peters (1954:28), this snake is diurnal and feeds on teiid lizards.

Masticophis striolatus striolatus Mertens

Coluber striolatus Mertens, Zoologica (Stuttgart), 32:190, 1934.—Substitute name for *Coluber lineatus* Bocourt, a secondary homonym of *Coluber lineatus* Linnaeus = *Lygophis lineatus.* Type locality restricted to Presidio de Mazatlán, Sinaloa, México, by Smith and Taylor (1950a:343).

Masticophis striolatus striolatus, Zweifel and Norris, Amer. Midl. Nat., 54: 242, July, 1955.

Apatzingán (4); Arteaga; Coalcomán (3); El Sabino; Jiquilpan; La Palma; La Playa (3); Lombardia; Nueva Italia; Río Cachán; Santa Ana; Uruapan (2); Volcán Jorullo; Ziracuaretiro.

This large diurnal species inhabits open scrub forest and cultivated terrain from sea level to about 1650 meters. On the Mexican Plateau it is known from the area around Lago de Chapala, to which it possibly gained access through the valleys in the headwaters of the Tepalcatepec drainage. Specimens from southern Michoacán have been reported previously by Peters (1954:28) and Duellman (1954b: 16) as *Masticophis flagellum lineatus.*

Masticophis taeniatus australis Smith

Masticophis taeniatus australis Smith, Jour. Washington Acad. Sci., 31:390, September 11, 1941.—Guanajuato, Guanajuato, México.

Tacícuaro (2); Zamora.

This species reaches the southern limit of its distribution in the state of Michoacán. The limited ecological data available suggest that the species inhabits the open mesquite grassland of the Mexican Plateau.

Oxybelis aeneus auratus (Bell)

Dryinus auratus Bell, Zool. Jour., 2:324, 1825.—México. Type locality restricted to Tehuantepec, Oaxaca, México, by Smith and Taylor (1950a: 340).

Oxybelis aeneus auratus, Bogert and Oliver, Bull. Amer. Mus. Nat. Hist., 83:381, March 30, 1945.

Coahuayana; El Sabino (4); between Las Tecatas and Las Higuertas; between Los Pozos and La Ciénega; Playa Azul; Pómaro (2); between Pómaro and Maruata (2); Punto San Telmo; Río Tizupan.

On the basis of the number of specimens seen and collected on the seaward slopes of the Sierra de Coalcomán, this is a common snake

there. Most specimens were collected in tropical semi-deciduous forest; others were collected in oak forest to an elevation of 1700 meters. Apparently *Oxybelis* does not inhabit the lower parts of the Tepalcatepec Valley; the only specimens from the inland area are four from El Sabino, which is situated at about 900 meters on the slopes of the Cordillera Volcánica. One individual was seen in gallery forest near Limoncito at an elevation of 730 meters on the northern slopes of the Sierra de Coalcomán.

Pituophis deppei deppei (Duméril)

Elaphis deppei Duméril, Mem. Acad. Inst. France, 23:453, 1835.—México. Type locality restricted to San Juan Teotihuacán, México, México, by Smith and Taylor (1950a:334).

Pituophis deppei deppei, Stull, Occ. Pap. Mus. Zool. Univ. Michigan, 250:1, October 12, 1932.

Carapan (2); Morelia; Tacambaro; Tacícuaro; Zacapu.

Duellman (1960b) showed that the widespread species *Pituophis deppei* was composite and that the "lined subspecies" actually represented another species, *Pituophis lineaticollis*. *Pituophis deppei* occurs only on the Mexican Plateau; in Michoacán it inhabits mesquite grassland and oak-bunch grass associations between 1900 and 2200 meters.

Pituophis lineaticollis lineaticollis (Cope)

Arizona lineaticollis Cope, Proc. Acad. Nat. Sci. Philadelphia, 13:300, December 28, 1861.—Southern Mexican Plateau. Type locality restricted to 24 kilometers northwest of Oaxaca, Oaxaca, México, by Duellman (1960b:607).

Pituophis lineaticollis lineaticollis, Duellman, Univ. Kansas Publ. Mus. Nat. Hist., 10:607, May 2, 1960.

Acuaro de las Lleguas; Dos Aguas (3); Morelia; Tancítaro (5).

This species reaches the northern limits of its range in the Sierra de Coalcomán and on the Mexican Plateau in Michoacán. On the plateau it has been collected in mesquite grassland at elevations between 1500 and 2000 meters. In the Sierra de Coalcomán individuals were found in open pine-oak forest at 2100 meters elevation and in a meadow surrounded by pine-oak forest at 2300 meters.

Pseudoficimia frontalis (Cope)

Toluca frontalis Cope, Proc. Acad. Nat. Sci. Philadelphia, 16:167, September 30, 1864.—Colima, Colima, México.

Pseudoficimia frontalis, Günther, Biologia Centrali-Americana, Reptilia, p. 96, May, 1893.

Apatzingán; Coalcomán (6); El Sabino (2).

Most specimens were found beneath rocks in grassy areas near the upper limits of the arid scrub forest, both in the Sierra de

Coalcomán and on the southern slopes of the Cordillera Volcánica; all are from elevations of less than 1100 meters. One specimen was found on a road at night near Apatzingán. This species has been found in similar habitats near Huajintlán, Guerrero, and in arid scrub forest at lower elevations in Colima. It is unknown from the coast of Michoacán.

Pseudoficimia pulcherrima Taylor and Smith

Pseudoficimia pulcherrima Taylor and Smith, Univ. Kansas Sci. Bull., 28:246, May 15, 1942.—Huajintlán, Guerrero, México.

Apatzingán.

This specimen (CNHM 39208) was reported by Schmidt and Shannon (1947:81); they stated that it was a paratype of *P. pulcherrima.* However, Taylor and Smith (1942a:246) did not mention the specimen; aside from the type (EHT-HMS 5497), the only other specimen they designated as belonging to the type series was UMMZ 85711 from Chilpancingo, Guerrero.

The taxonomic validity of *Pseudoficimia pulcherrima* remains doubtful, for only minor characters distinguish it from *P. frontalis.* Furthermore, all known specimens of *P. pulcherrima* are from within the geographic range of *P. frontalis.*

Rhadinaea hesperia hesperia Bailey

Rhadinaea hesperia Bailey, Occ. Pap. Mus. Zool. Univ. Michigan, 412:8, May 6, 1940.—Omilteme and Sierra de Burro, Guerrero. Type locality restricted to Omilteme, Guerrero, México, by Smith and Taylor (1950a: 332).

Rhadinaea hesperia hesperia, Smith, Proc. Biol. Soc. Washington, 55:185, December 31, 1942.

Arteaga (3); Coalcomán; El Sabino (2); Uruapan; Volcán Jorullo (2).

One specimen from Volcán Jorullo (UMMZ 104494), three from Arteaga (UMMZ 119281), and one from Uruapan (UMMZ 92342) are typical of the subspecies *R. h. hesperia* in possessing a lateral cream-colored line on the sixth and parts of the fifth and seventh dorsal scale rows and in lacking a dark line on the second scale row. The specimens from El Sabino (EHT-HMS 5441 and UIMNH 18933) and one from Coalcomán (UMMZ 104502) have the cream-colored line on the sixth and adjacent parts of the fifth and seventh scale rows and have a dark line on the second scale row. Another individual from Volcán Jorullo (UMMZ 104682) has cream-colored lines like the others, but it possesses two lateral dark lines, one on the second scale row, and one on the third.

Smith (1942d:186) diagnosed *Rhadinaea hesperia hesperioides* as differing from the nominal subspecies in having the cream-colored line on the fourth and fifth scale rows and in possessing a dark line on the second scale row. The specimens seen all have the lateral cream-colored line centered on the sixth scale row, as is characteristic of *R. h. hesperia.* Although many of the specimens also possess a dark line on the second scale row, these specimens are here assigned to *R. h. hesperia.* Additional specimens are necessary to define accurately the subspecies and their ranges. Peters (1954:29) assigned the specimens from Coalcomán to *R. h. hesperioides.*

In life the specimens from Arteaga had bright cream-colored temporal stripes and dorsolateral stripes on the anterior part of the body. The chin and anterior one-sixth of the belly was white; posteriorly the venter was bright orange-red.

In Michoacán this snake has been found in tropical semi-deciduous forest, arid scrub forest, and pine-oak forest at elevations from 850 to 1500 meters.

Rhadinaea laureata (Günther)

Dromicus laureatus Günther, Ann. Mag. Nat. Hist., ser. 4, 1:419, 1868.—Mexico City.

Rhadinaea laureata, Boulenger, Catalogue Snakes . . . British Museum, 2, p. 179, September 23, 1894.

Capácuaro; Carapan (8); Cherán (3); Paracho (2); Pátzcuaro; Tancítaro (10).

This snake is abundant in the Cordillera Volcánica, but it is unknown in the mountains to the northeast of Morelia or in the Sierra de Coalcomán. Most specimens were found beneath volcanic rocks imbedded in the ashy soil in pine forest between 1800 and 2300 meters.

Rhadinaea taeniata (Peters)

Dromicus taeniatus Peters, Monats. Akad. Wiss. Berlin, p. 275, 1863.—México.

Rhadinaea taeniata, Bailey, Occ. Pap. Mus. Zool. Univ. Michigan, 412:14, May 6, 1940.

Tancítaro (2).

This species, which is known only from a small region in the mountains of Jalisco and central Michoacán, is represented by two specimens (CNHM 37130 and 39030) collected at Tancítaro (see Schmidt and Shannon, 1947:80).

Salvadora bairdi Jan

Salvadora Bairdii Jan. Icon. gener. ophid., livr. 2, pl. 3, fig. 2, 1860.—México. Type locality restricted to Acámbaro, Guanajuato, México, by Smith and Taylor (1950a:330).

Barranca Seca; Carapan; Cerro San Andrés; Cojumatlán (2); Jiquilpan; Morelia; Pátzcuaro (4); Quiroga; Sahuayo (2); Tacícuaro (12); Tancítaro (56); Uruapan (2); Zacapu (2); between Zitácuaro and Tuxpan (3).

This species is abundant on the Mexican plateau, where it inhabits the more grassy areas in the mesquite grassland and cutover land in the pine forests from 1550 to 2500 meters. Davis and Dixon (1957:21) described a specimen from Zacapu as having two dark paravertebral stripes diverging on the temporals and extending through the eye onto the loreal, a characteristic of *Salvadora lineata.* On the basis of this specimen, Davis and Dixon suggested that *Salvadora bairdi* and S. *lineata* were subspecifically related. The examination of the large number of specimens from Michoacán has revealed this kind of coloration in only one other specimen, an individual from Tacícuaro, in which the stripes diverge, but do not extend through the eye onto the loreal. Data on scutellation for the large series from Tancítaro were given by Schmidt and Shannon (1947:78), and for the series from Tacícuaro by Smith (1943:466).

Salvadora mexicana (Duméril, Bibron, and Duméril)

Zamenis mexicanus Duméril, Bibron, and Duméril, Erpétologie générale, 7 (pt. 1), p. 695, 1854.—Cape Corrientes, Jalisco, México.

Salvadora mexicana Günther, Ann. Mag. Nat. Hist., ser. 3, 12:349, 1863.

Apatzingán (12); Capirio (2); El Sabino (5); Huetamo; La Placita; La Playa (4); Lombardia; Nueva Italia; Ojos de Agua de San Telmo; Oropeo; Río Cancita, 14 km. E of Apatzingán; Santa Ana.

This is one of the most abundant snakes in the arid lowlands of the Tepalcatepec Valley; observations indicate that it probably is equally abundant on the coastal lowlands. Near Apatzingán as many as five of these snakes have been seen in one-half hour. The snakes seem to be equally abundant and active in the dry season and in the rainy season. Most individuals were seen on the ground, but two were found in low trees. On several occasions *Salvadora mexicana* was observed in pursuit of lizards on the ground. Captured individuals regurgitated *Cnemidophorus costatus zweifeli, Cnemidophorus deppei infernalis, Sceloporus horridus oligoporus, Sceloporus pyrocephalus,* and *Urosaurus gadowi.*

Salvadora mexicana inhabits only the arid scrub forest at elevations from sea level to about 1000 meters.

Sibon nebulatus (Linnaeus)

Coluber nebulatus Linnaeus, Systema naturae, ed. 10, 1, p. 222, 1758.—Africa (in error). Type locality restricted to Jicaltepec, Veracruz, México, by Smith and Taylor (1950a:349).

Sibon nebulatus, Taylor, Univ. Kansas Sci. Bull., 26:473, November 27, 1940.

Aquila.

The one specimen from Michoacán was collected by Peters (1954: 30) in tropical semi-deciduous forest on the coastal foothills of the Sierra de Coalcomán. As presently known, the range of this species in western México extends from Chiapas to Nayarit. Throughout this region the species avoids scrub forest; this may explain its absence in the Balsas-Tepalcatepec Valley.

Sonora michoacanensis michoacanensis (Dugès)

Contia michoacanensis Dugès, *in* Cope, Proc. Amer. Philos. Soc., 22:178, 1885.—Michoacán. Type locality restricted to Apatzingán, Michoacán, México, by Smith and Taylor (1950a:335).

Sonora michoacanensis michoacanensis, Stickel, Proc. Biol. Soc. Washington, 56:116, October 19, 1943.

Apatzingán (3); Coalcomán (3); 12 km. S of Tzitzio.

These specimens, together with all known specimens from the Sierra del Sur in Guerrero (KU 23790-1, MVZ 45123) and the upper Balsas Basin in Puebla (UIMNH 41688), are referable to *S. m. michoacanensis*. The dorsal pattern consists of a highly variable number of cross-bands of red, white, and black. In the specimens from Michoacán there are as many as 17 red cross-bands on the body. One specimen from Apatzingán (CNHM 37141) has just behind the head a white band, bordered on either side by a narrow black band; posteriorly the body is uniform red. Two specimens from Coalcomán (UMMZ 109905-6) have respectively 11 and 13 red cross-bands and 20 and 17 white cross-bands, and the posterior part of the body is devoid of red color. Other specimens from these localities have red, black, and white cross-bands throughout the length of the body.

Sonora michoacanensis michoacanensis is distinguished from *S. michoacanensis mutabilis* by the presence of cross-bands on the tail in the latter (Stickel, 1943:116). One specimen from Coalcomán (UMMZ 109904) has one narrow band on the tail; all others from Michoacán have uniformly red tails.

Apparently *Sonora michoacanensis michoacanensis* ranges in semi-arid and arid habitats from the upper Balsas Basin in Puebla westward to the lower slopes of the Sierra de Coalcomán, whereas *S. m.*

mutabilis lives in foothills of the Sierra Madre Occidental from southern Jalisco to Nayarit. Zweifel (1959b:6) presented evidence to show that specimens of *S. m. mutabilis* supposedly from "Distrito Federal" probably bear erroneous locality data.

Tantilla bocourti (Günther)

Homalocranium bocourti Günther, Biologia Centrali-Americana, Reptilia, p. 149, 1895.—Guanajuato, Guanajuato, México.

Tantilla bocourti, Cope, Amer. Nat., 30:1021, December, 1896.

Carapan; Pátzcuaro (2); between Zitácuaro and Río Tuxpan (11).

This small snake is an inhabitant of the coniferous forests and the pine-oak forests on the Cordillera Volcánica. Data on the series from between Zitácuaro and the Río Tuxpan were given by Taylor (1940c:481).

Tantilla calamarina Cope

Tantilla calamarina Cope, Proc. Acad. Nat. Sci. Philadelphia, 18:320, February 13, 1867.—Guadalajara, Jalisco, México.

Apatzingán; La Placita.

Although this snake has been collected at high elevations along the rim of the Mexican Plateau in Nayarit, Jalisco, México, and Puebla, the specimens from Michoacán are from arid scrub forest at elevations of less than 400 meters. The species has been found in similar habitats in Colima (Oliver, 1937:24) and in Sinaloa and the Tres Marías Islands (Zweifel, 1960:110).

Toluca lineata lineata Kennicott

Toluca lineata Kennicott, *in* Baird, Report on the United States and Mexican boundary survey, 2, Reptiles, p. 23, 1859.—Valley of México.

Toluca lineata lineata, Taylor and Smith, Univ. Kansas Sci. Bull., 28:343, May 15, 1942.

Capácuaro; Carapan (12); Cherán (23); Cojumatlán; Los Reyes; Morelia (2); Nahuatzen; Paracho (10); Pátzcuaro (17); Uruapan (2).

This small snake is an inhabitant of the coniferous forests between elevations of about 1550 and 2800 meters. Not infrequently, individuals have been found in pine-oak forest within these elevations.

The generic status of *Toluca* is unsettled. Taylor and Smith (1942b) separated *Toluca* from *Conopsis* by the presence of enlarged and grooved posterior maxillary teeth in *Toluca* and their absence in *Conopsis.* Bogert and Oliver (1945:378) suggested synonymizing *Toluca* with *Conopsis.* Smith and Laufe (1945:12) defined the generic position of *Toluca.* Actually, in deciding the generic position of these snakes, five genera (*Ficimia, Gyalopion, Pseudoficimia, Conopsis,* and *Toluca*) must be considered. Of these

Ficimia and *Gyalopion* are closely related; they have been placed in one genus by some workers. *Pseudoficimia* is intermediate between *Ficimia-Gyalopion* and *Toluca-Conopsis*. A workable definition of the supraspecific classification of these snakes must await a thorough review of the species.

Trimorphodon biscutatus biscutatus (Duméril, Bibron, and Duméril)

Dipsas biscutata Duméril, Bibron, and Duméril, Erpétologie générale, 7 (pt. 2):1153, 1854.—México. Type locality restricted to Tehuantepec, Oaxaca, México, by Smith and Taylor (1950a:340).

Trimorphodon biscutatus biscutatus, Smith, Proc. U. S. Natl. Mus., 91:159, November 10, 1941.

Apatzingán (11); Cofradía; Cuatro Caminos; El Sabino (2); La Placita; La Playa (2); Lombardia (2); Nueva Italia (2); Río Tepalcatepec, 27 km. S of Apatzingán; Tafetán.

In the arid lowlands of the Tepalcatepec Valley and presumably also in the scrub forest of the coastal lowlands, this is an abundant snake, which is active only at night. Usually snakes of this species are found on the ground, but one large individual was observed at night in a low tree. That individual defied capture by widely opening its mouth and striking repeatedly at the collector. The excreta of one specimen contained feathers of an unidentified species of bird.

Trimorphodon latifascia Peters

Trimorphodon biscutata latifascia Peters, Monats. Akad. Wiss. Berlin, p. 877, 1869.—Puebla, México. Type locality restricted to Izúcar de Matamoros, Puebla, México, by Smith and Taylor (1950a:341).

Trimorphodon latifascia, Taylor, Univ. Kansas Sci. Bull., 25:364, July 10, 1939.

Apatzingán (5); Casada Tzararacua; Coalcomán (2); Lombardia; 14 km. S of Lombardia; Nueva Italia; San Salvador.

In Michoacán this species has been collected in semi-arid habitats at elevations from 300 to 1430 meters in the Tepalcatepec Valley and lower slopes of the Cordillera Volcánica. In this area it occurs sympatrically with *Trimorphodon biscutatus biscutatus*.

In life, adults have a pale tan dorsal ground color and rich chocolate brown cross-bands; the eye is pale grayish tan. A juvenile from Coalcomán has black cross-bands on a pale grayish tan ground color. As stated by Schmidt and Shannon (1947:83) and Peters (1954:32), the type specimen of *Trimorphodon fasciolata* Smith from Cascada Tzararacua is indistinguishable from specimens of *Trimorphodon latifascia*.

Seven males have 209 to 223 (216.5) ventrals; one female has 227 ventrals. The number of dark cross-bands on the body varies from 12 to 16 (13.5). The relationships of this species are with

Trimorphodon tau on the Mexican Plateau. In fact, additional specimens from the headwaters of the Tepalcatepec Valley and the lower slopes of the Mexican Plateau in eastern Michoacán and adjacent Jalisco may show that the two are conspecific. *Trimorphodon latifascia* differs from *tau* in having fewer dark crossbands on the body and in lacking an interocular bar.

Trimorphodon tau Cope

Trimorphodon tau Cope, Proc. Amer. Philos. Soc., 11:151, 1869.—Quiotepec, Oaxaca, México.

Emiliano Zapata (2); between Morelia and Ciudad Hidalgo; Tacícuaro; Tangamandapio.

Two of the specimens from Michoacán (UMMZ 118948 from Tangamandapio and UIMNH 19138 from Tacícuaro) have cream-colored, Y-shaped marks on the head. These markings supposedly are characteristic of *Trimorphodon upsilon.* One specimen from Emiliano Zapata (UMMZ 118950) and one from between Morelia and Ciudad Hidalgo (EHT-HMS 21402) have a cream-colored line on the parietal suture; in another specimen from Emiliano Zapata (UMMZ 118949) the anterior end of this line is expanded, giving the appearance of an incipient "Y". Thus, the nature of the markings on the head in specimens from Michoacán is intermediate between the typical condition in *Trimorphodon tau* and the usual condition in *T. upsilon.* Smith and Taylor (1945:148) gave the range of *Trimorphodon tau* as: "Central Guerrero, in the Sierra Madre del Sur; central Oaxaca; and the edge of the plateau in central Michoacán." They gave the range of *Trimorphodon upsilon* as: "Southern Chihuahua south to central Michoacán, east to central Hidalgo." Specimens referable to *T. tau* have been found at La Joya de Salas, near Ciudad Victoria, and near Llera, Tamaulipas (see Smith and Darling, 1952:85, and Martin, 1958:74). Some of these specimens also show combinations of characteristics of *T. tau* and *T. upsilon.* Smith and Darling (*loc. cit.*) suggested that *T. tau* and *T. upsilon* be considered as subspecies. However, if *T. tau* and *T. upsilon* are subspecies, intergrades would be expected between the ranges of the two populations and not on the northeastern and southwestern periphery of their combined ranges. Instead, the limited evidence now available suggests that *T. tau* and *T. upsilon* are names based on a highly variable character of color pattern of the head, and that only one species is involved.

In Michoacán this species inhabits the mesquite grassland on the Mexican Plateau.

Tropidodipsas occidentala Oliver

Tropidodipsas occidentala Oliver, Occ. Pap. Mus. Zool. Univ. Michigan, 360:20, November 20, 1937.—Comala, Colima, México.

Coalcomán.

This specimen was reported by Peters (1954:34), who found it beneath a rock at the mouth of a heavily wooded ravine near Coalcomán at an elevation of 950 meters. The only other known specimen is from Comala, Colima, a village, like Coalcomán, that is located near the upper limits of the arid scrub forest.

Natrix valida isabelleae Conant

Natrix valida isabelleae Conant, Nat. Hist. Misc., 126:7, September 15, 1953. —Pie de la Cuesta, Laguna Coyuca, Guerrero, México.

Coahuayana; Playa Azul (2); Punto San Juan de Lima.

Three females and one male have, respectively, 133, 135, 135, and 131 ventrals, and 68, 68, 73, and 75 caudals. The grayish stippling on the posterior ventral surfaces mentioned by Conant (1953:9) is not visible on these specimens. In the small individuals from Punto San Juan de Lima and from Coahuayana there are four longitudinal rows of dark spots on the dorsum; in two large females from Playa Azul the spots are barely discernible.

All of the specimens from Michoacán were found in the coastal lowlands; those from Playa Azul were collected from a small brackish, mangrove-lined lagoon.

Storeria storerioides (Cope)

Tropidoclonium storerioides Cope, Proc. Acad. Nat. Sci. Philadelphia, 17:190, December 26, 1865.—Mexican Plateau. Type locality restricted to Tres Cumbres, Morelos, México, by Smith and Taylor (1950a:336).

Storeria storerioides, Garman, Mem. Mus. Comp. Zool., 8(3):29, June, 1883.

Dos Aguas (11); Puerto de Garnica; Tancítaro (11); Tzitzio; Uruapan; 16 km. NW of Zacapu.

Three males and six females from the Sierra de Coalcomán have, respectively, 122-128 (125.3) and 126-136 (130.0) ventrals, and 46-47 (46.7) and 38-42 (39.1) caudals. Four males and eleven females from the Cordillera Volcánica have, respectively, 124-132 (128.5) and 127-139 (136.4) ventrals, and 43-48 (44.7) and 38-44 (40.2) caudals. These data show that, although there is little difference in the number of caudals, specimens from the Sierra de Coalcomán have fewer ventrals than do specimens from the Cordillera Volcánica. Of eleven specimens from the Sierra de Coalcomán, two have black bellies. Five others from the Sierra de Coalcomán and one from Puerto de Garnica in the Cordillera Volcánica have

the bellies heavily stippled with black, giving a gray appearance. Melanistic tendencies in this species have been discussed by Anderson (1960:64), who examined the specimen from Tzitzio. In life, one specimen from Dos Aguas (UMMZ 119451) had a cream-colored belly; the edges of the ventrals were dark brick-red.

In Michoacán this snake inhabits pine-oak, pine, and fir forests at elevations between 1550 and 2800 meters in the Cordillera Volcánica and the Sierra de Coalcomán. Most specimens were found beneath rocks; the one from Tzitzio was removed from the stomach of a Mexican Motmot (Anderson, 1960:66).

Thamnophis dorsalis cyclides Cope

Thamnophis cyrtopsis cyclides Cope, Proc. Acad. Nat. Sci. Philadelphia, 13:299, December 28, 1861.—Cape San Lucas, Baja California (in error). Type locality restricted to Guanajuato, Guanajuato, México, by Smith and Taylor (1950a:330). Smith, Copeia, no. 2:140, June 8, 1951. Milstead, Texas Jour. Sci., 5:368, September, 1953.

Thamnophis eques eques (*nec.* Reuss), Smith, Zoologica, 27:106, October 23, 1942. Bogert and Oliver, Bull. Amer. Mus. Nat. Hist., 83:356, March 30, 1945.

Thamnophis vicinus Smith, Zoologica, 27:104, October 23, 1942.—Temazcal, Michoacán, México.

Thamnophis dorsalis cyclides, Fitch and Milstead, Copeia, no. 1:112, March 17, 1961.

Barolosa; Coalcomán; Dos Aguas (3); Los Reyes; Morelia (16); Opopeo; Pino Gordo; Tacícuaro (16); Tancítaro (14); Tangamandapio (2); Temazcal (2); Tzintzuntzan; Uruapan.

The snakes comprising the former *Thamnophis eques*-group have undergone extensive taxonomic and nomenclatural shuffling by Smith (1942 and 1951), Bogert and Oliver (1945), Milstead (1953), and Fitch and Milstead (1961). Smith recognized in Michoacán three members of the *T. eques* (= *dorsalis*) complex: *eques eques, eques postremus,* and *vicinus.* Later, Smith (1951) showed that the specific name *eques* had been misapplied, so that *T. eques eques* became *T. cyrtopsis cyclides,* and *T. eques postremus* became *T. cyrtopsis postremus;* under this arrangement *T. vicinus* stood unchanged. In the meantime, Bogert and Oliver (1945:359) presented a reinterpretation of Smith's data and suggested that *T. vicinus,* which differs from *T. dorsalis cyclides* only in lacking a middorsal stripe, ". . . is not a species, but only a pattern phase, possibly a simple mutant of *T. e. eques*" (= *T. dorsalis cyclides,* by present arrangement). Milstead (1953) agreed with Bogert and Oliver on the status of *T. vicinus;* furthermore, on the basis of only a few specimens, Milstead concluded

that *T. cyrtopsis postremus* was not subspecifically distinct from *T. cyrtopsis cyclides.* Recently, Fitch and Milstead (1961) showed that *Thamnophis dorsalis* Baird and Girard (1853) was the correct name for the snakes that had been recognized as *Thamnophis cyrtopsis* Kennicott (1860). Consequently, the snakes referred to *T. eques eques* by Smith (1942) and to *T. cyrtopsis cyclides* by Smith (1951) and Milstead (1953) are now *T. dorsalis cyclides.*

Aside from one specimen from Temazcal and nine from Morelia (paratypes of *T. vicinus*), only two other specimens completely lacking the middorsal stripe have been seen; one is a male (UMMZ 102510) having 161 ventrals and an incomplete tail from Pino Gordo, and the other is a male (CNHM 39060) from Tancítaro having 158 ventrals and an incomplete tail. A female from Tancítaro (CNHM 39061) having 153 ventrals and 77 caudals has no lateral stripes and only a narrow middorsal stripe on the anterior part of the body. Throughout the region where *T. vicinus*-like snakes have been found, typical *T. dorsalis cyclides* occurs in much greater numbers. I concur with Bogert and Oliver in placing *T. vicinus* as a synonym of *T. dorsalis cyclides.*

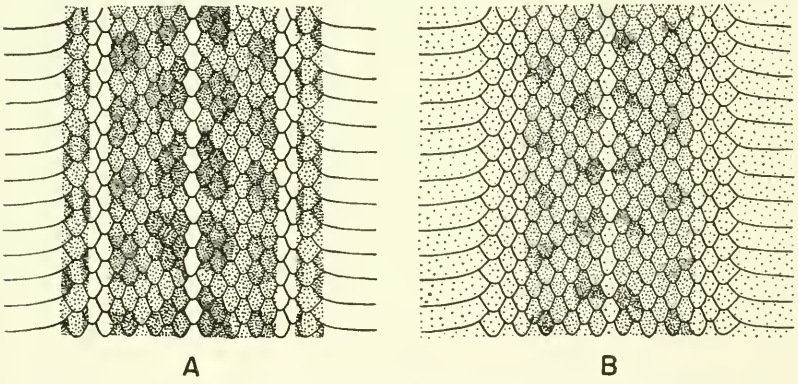


FIG. 10. Dorsal color pattern of *Thamnophis dorsalis cyclides* (A) and *Thamnophis dorsalis postremus* (B).

Milstead (1953) had available few specimens of *Thamnophis dorsalis* from the Tepalcatepec Valley. The large series now in existence shows that the population in the Tepalcatepec Valley differs distinctly from that inhabiting the Mexican Plateau, Cordillera Volcánica, and Sierra de Coalcomán. Therefore the name *T. dorsalis postremus* Smith (1942) is resurrected for the population

in the Tepalcatepec Valley. *T. dorsalis cyclides* and *T. dorsalis postremus* differ in color pattern (Fig. 10) and in scutellation (Table 6). Specimens from the Mexican Plateau and mountain ranges have a distinct light stripe on the second and third scale rows, a dark brown dorsum having squarish black spots, and a row of dark spots on the first row of dorsal scales. Specimens from the Tepalcatepec Valley have a grayish brown dorsum having smaller and less distinct dark spots and no light stripe on the second and third scale rows; the first, second, and third rows of scales are colored like the venter. In some specimens there are small dark flecks on the first row of dorsal scales.

TABLE 6.—VARIATION IN SCUTELLATION IN THAMNOPHIS DORSALIS.

CHARACTER			Mexican Plateau	Sierra de Coalcomán	Tepalcatepec Valley
Ventrals.....	♂	N	31	2	32
		Mean	164.0	156.5	144.6
		Range	153–171	154–159	138–151
	♀	N	19	2	32
		Mean	153.5	154.7	138.3
		Range	149–159	149–159	131–141
Caudals.....	♂	N	28	2	29
		Mean	83.8	81.0	73.4
		Range	80–100	79–83	70–79
	♀	N	14	2	28
		Mean	78.0	72.0	68.5
		Range	71–87	72	63–73

One specimen from Uruapan (1550 meters) and one from Coalcomán (950 meters) are intermediate in color pattern between *T. dorsalis cyclides* and *T. dorsalis postremus*. Both have indistinct lateral stripes and only small dark spots below the stripes. In scutellation these specimens are like *T. dorsalis cyclides*.

In Michoacán *Thamnophis dorsalis cyclides* has been collected in a variety of habitats on the Mexican Plateau: pine-oak forest, fir forest, marshes, and cleared land from 1550 to 2800 meters. In the Sierra de Coalcomán one was taken in broad-leafed forest at 950 meters, three in pine-oak forest at 2100 meters, and one in pine forest at 2300 meters.

Thamnophis dorsalis postremus Smith

Thamnophis eques postremus Smith, Zoologica, 27:109, October 23, 1942.—El Sabino, Michoacán, México.

Thamnophis cyrtopsis postremus Smith, Copeia, no. 2:140, June 8, 1951.

Thamnophis cyrtopsis cyclides (part), Milstead, Texas Jour. Sci., 5:368, September, 1953.

Thamnophis dorsalis postremus, Fitch and Milstead, Copeia, no. 1:112, March 17, 1961.

Apatzingán (31); Capirio (2); Charapendo; Cuatro Caminos (22); El Sabino; Lombardia (9); Nueva Italia (8); Uruapan (3).

The reasons for recognizing the population of *Thamnophis dorsalis* in the Tepalcatepec Valley as distinct from that on the surrounding highlands are presented in the discussion of *Thamnophis dorsalis cyclides.* In certain features of coloration and in the low numbers of ventrals and caudals, *T. dorsalis postremus* shows more resemblance to *T. dorsalis sumichrasti* than to *T. dorsalis cyclides.* According to Milstead (1953:367), *T. dorsalis cyclides* ranges southward from the Río Balsas in southwestern México. If specimens could be obtained from the upper Balsas Basin they might show that *T. dorsalis postremus* inhabits that extensive basin.

In the Tepalcatepec Valley *T. dorsalis postremus* is most frequently found at night in the rainy season, at which time the snakes are abundant near temporary pools where frogs are breeding. The absence of specimens from the coastal lowlands of Guerrero, Michoacán, and Colima indicate that, although the species inhabits the lowlands of the Tepalcatepec Valley, its range does not include the coastal lowlands.

A female (UMMZ 119402 from Cuatro Caminos) having 139 ventrals and a body length of 576 mm., on June 20, 1958, gave birth to 25 young, of which 18 (9 males and 9 females) were preserved. In body length the males varied from 132 to 141 (137.3) mm.; the females, 125 to 137 (133.1) mm. In tail length the males varied from 38 to 44 (42.4) mm.; females, 35 to 42 (39.7) mm. The males have 138 to 147 (142.2) ventrals and 70 to 75 (72.9) caudals; females have 131 to 140 (135.8) ventrals and 63 to 71 (67.0) caudals.

Thamnophis eques eques (Reuss)

Coluber eques Reuss, Zool. Misc., p. 152, 1834.—México. Type locality restricted to Guadalajara, Jalisco, México, by Smith and Taylor (1950a: 334).

Thamnophis macrostemma macrostemma, Smith and Taylor, Bull. U. S. Natl. Mus., 187:163, October 5, 1945.

Thamnophis subcarinata subcarinata, Smith, Herpetologica, 5:63, May 31, 1949.

Thamnophis eques eques, Smith, Copeia, no. 2:139, June 8, 1951.

Jiquilpan; Lago de Cuitzeo; Lago de Pátzcuaro (17); Pátzcuaro (5); Tangancícuaro; Tupátaro (2); Undameo; Zacapu.

Although this snake has been collected in open pine-oak forest and in oak-bunch grass associations, it seems to reach its greatest abundance in marshes on the Mexican Plateau at elevations of 1550 to 2300 meters.

Thamnophis melanogaster canescens Smith

Thamnophis melanogaster canescens Smith, Zoologica, 27:117, October 23, 1942.—Chapala, Jalisco, México.

Lago de Cuitzeo (5); Lago de Pátzcuaro; Pátzcuaro; Tacícuaro; Tangamandapio (2).

This species of garter snake seems to be most abundant in the marshes adjacent to the lakes on the Mexican Plateau in Michoacán and Jalisco. At these elevations (1550 to 2200 meters) it often is found in association with *Thamnophis eques eques* and sometimes with *Thamnophis dorsalis cyclides.* On June 11, 1958, individuals of this species were found in a hyacinth-choked marsh at Tangamandapio at night.

One specimen from Tangamandapio (UMMZ 119414) had, in life, a dark chocolate brown dorsum, reddish brown sides, and cream-colored belly, chin, and labials. There were no longitudinal dorsal stripes.

Thamnophis scalaris scaliger (Jan)

Tropidonotus scaliger Jan, Elenco sistematico degli Ofidi, p. 70, 1863.—No type locality designated. Type locality restricted to Mexico City, Distrito Federal, by Smith and Taylor (1950a:329).

Thamnophis scalaris scaliger, Smith, Zoologica, 27:103, October 23, 1942.

Cerro Tancítaro (2); Nahuatzen; Opopeo; 26 km. S of Pátzcuaro.

The few specimens of this species from Michoacán have been collected at elevations from 1800 to 3400 meters in pine or fir forest in the Cordillera Volcánica.

Micrurus distans michoacanensis (Dugès)

Elaps diastema michoacanensis Dugès, La Naturaleza, ser. 2, 1:487, 1891. —Michoacán. Type locality restricted to Apatzingán, Michoacán, México, by Smith and Taylor (1950a:335).

Micrurus distans michoacanensis, Zweifel, Amer. Mus. Novitates, 1953:11, June 26, 1959.

Apatzingán (6).

All specimens were collected in the arid scrub forest of the Tepalcatepec Valley. The number of black rings on the body varies from six to eleven. In this respect they agree with the diagnosis of this subspecies presented by Zweifel (1959b:9).

Micrurus laticollaris (Peters)

Elaps marcgravii laticollaris Peters, Monats. Akad. Wiss. Berlin, p. 877, 1869.—Izúcar de Matamoros, Puebla, México.

Micrurus laticollaris, Schmidt, Publ. Field Mus. Nat. Hist., zool. ser., 20:39, December 11, 1933.

El Sabino (2); Lombardia.

This species ranges throughout the Balsas-Tepalcatepec Basin westward into Colima; specimens from Michoacán were collected in arid scrub forest at elevations from 500 to 1050 meters. The limited observations on *Micrurus distans michoacanensis* and *M. laticollaris* indicate that, at least in the Tepalcatepec Valley, *M. laticollaris* seems to inhabit slightly more mesic areas than does *M. distans michoacanensis*.

Pelamis platurus (Linnaeus)

Anguis platura Linnaeus, Systema naturae, ed. 12, 1:391, 1766.—Pine Island, Pacific Ocean.

Pelamis platurus, Gray, Ann. Philos., p. 15, 1825.

Boca de Apiza.

In November, 1955, Alfonzo Gonzales, a geographer from the University of Texas, observed sea snakes on the beaches of Michoacán. In May, 1956, Donald D. Brand of the University of Texas gave me one specimen of *Pelamis platurus* that he obtained on March 2, 1956, at Boca de Apiza. Furthermore, he supplied me with the following observations based on his field work along the coast of Michoacán from the Río Coahuayana to Maruata from March 1, to April 15, 1956. At that time many sea snakes were observed; in some places living and dead individuals were seen on the beaches; innumerable snakes were seen in the surf. When live individuals were taken from the beach and thrown into the ocean, they usually swam to shore. Many partially eaten individuals were seen protruding from crab holes. Inquiries among the natives resulted in the following information: Sea snakes are frequently seen between November and April, but most commonly in March and April, at which time the water is cold. The natives referred to the sea snakes as "culebra del mar." Most natives said that the snakes were not poisonous; others did not know of any venomous properties. In May, 1956, I worked the coastal region from the Río Coahuayana to La Placita and saw no sea snakes. In the summer of 1950 James A. Peters, and in the summer of 1951 I worked nearly the entire coastal region of Michoacán; during

that time no *Pelamis* were seen. Insofar as I know, this is the first report of such seasonal activity in *Pelamis platurus* in the Americas.

Agkistrodon bilineatus bilineatus Günther

Ancisdrodon bilineatus Günther, Ann. Mag. Nat. Hist., ser. 3, 12:364, 1863. —Pacific coast of Guatemala.

Agkistrodon bilineatus bilineatus, Burger and Robertson, Univ. Kansas Sci. Bull, 34 (1):213, October 1, 1951.

Apatzingán; El Sabino; La Playa; Los Reyes.

All specimens from Michoacán are from inland localities between 300 and 1500 meters. The one from Los Reyes (USNM 46416) was collected by Nelson and Goldman on February 13, 1903. The elevation of Los Reyes (1500 meters) seems unusually high for this species, but otherwise there is no reason to doubt the authenticity of the record. Goldman (1951:192) in his description of Los Reyes stated: "Los Reyes is near the boundary between the Lower Austral and Arid Upper Tropical Zones but is preponderantly tropical in zonal character. The regular crops are mainly sugar cane, rice, and corn." Thus the biotic features of the area are not noticeably different from those at El Sabino and La Playa at lower elevations. The development of extensive agriculture through irrigation in the Tepalcatepec Valley and planting of rice and sugarcane in that area may produce a more widespread habitat for this snake.

The absence of specimens from the coastal lowlands is due solely to inadequate collecting; the natives there know the snake and report that it is not uncommon in certain areas.

Crotalus basiliscus basiliscus (Cope)

Caudisonia basilisca Cope, Proc. Acad. Nat. Sci. Philadelphia, September 30, 1864.—Colima. Type locality restricted to Colima, Colima, México, by Smith and Taylor (1950a:328).

Crotalus basiliscus basiliscus, Gloyd, Nat. Hist. Misc., 17:1, April 23, 1948.

Apatzingán (4); Camachines; Coalcomán; El Ticuiz.

Specimens from southern Michoacán have fewer ventrals and caudals than do those from the northern part of the range; three males and three females have, respectively, 178, 182, 182, 185, 186, and 188 ventrals, and 27, 28, 29, 22, 29, and 29 caudals. Klauber (1952:81) gave the following data for *Crotalus basiliscus* (based on specimens from the entire range, except Oaxaca): ventrals in males, 179-201 (191.4), in females, 185-206 (197.6); caudals in males, 26-36 (30.7), in females, 21-29 (24.4). Klauber (1952:84) remarked that the one specimen that he had seen from Apatzingán

had fewer ventrals and caudals than most other specimens. The low numbers of ventrals and caudals in specimens from Michoacán, as compared with more northern populations, may be indicative of a trend in the reduction of the numbers of these scutes from north to south. The southernmost examples of *Crotalus basiliscus* (*Crotalus basiliscus oaxacus* from Oaxaca) have 172-175 ventrals and 21 caudals (Gloyd, 1948).

In Michoacán *Crotalus basiliscus basiliscus* has been found in arid habitats on the coast, in the Tepalcatepec Valley, and in the lower parts of the Sierra de Coalcomán. All specimens are from localities below 1070 meters in elevation.

Crotalus durissus culminatus Klauber

Crotalus durissus culminatus Klauber, Bull. Zool. Soc. San Diego, 26:65, August 8, 1952.—El Sabino, Michoacán, México.

El Sabino (18).

These specimens are part of the type series and were collected by Hobart M. Smith near the upper limits of the arid scrub forest at an elevation of about 1050 meters on the lower slopes of the Cordillera Volcánica at the northern edge of the Tepalcatepec Valley. They were discussed in detail by Klauber (1952:66-70).

Crotalus intermedius intermedius Troschel

Crotalus intermedius Troschel, *in* von Müller, Reisen in Vereiningten Staaten, Canada und Mexico, vol. 3, p. 613, 1865.—Type locality unknown.

Crotalus intermedius intermedius, Klauber, Bull. Zool. Soc. San Diego, 26:9, August 8, 1952.

Cerro Tancítaro.

The one specimen is from the pine forests on the Cordillera Volcánica. At the present time this species is known from scattered localities in west-central Veracruz, Oaxaca, Michoacán, and as *Crotalus intermedius omiltemanus* in Central Guerrero. Apparently it is restricted to montane environments.

Crotalus molossus nigrescens Gloyd

Crotalus molossus nigrescens Gloyd, Occ. Pap. Mus. Zool. Univ. Michigan, 325:2, January 28, 1936.—Four miles west of La Colorada, Zacatecas, México.

Carapan; Los Conejos; Pátzcuaro; Tacícuaro (5).

In Michoacán this species has been found in pine forests between 1550 and 2300 meters in the Cordillera Volcánica. I expected to find it in the Sierra de Coalcomán, but inquiries among the natives living in the pine forests of that mountain range revealed that the people there have no knowledge of a large species of rattlesnake.

Crotalus polystictus (Cope)

Caudisonia polysticta Cope, Proc. Acad. Nat. Sci. Philadelphia, 17:191, December 26, 1865.—Tableland of México. Type locality restricted to Tupátaro, Guanajuata, México, by Smith and Taylor (1950a:330).

Crotalus polystictus Cope, *in* Yarrow, Wheeler's Rept. Geog. Geol. Expl. Surv. W. 100th. Mer., vol. 5, p. 533, 1875.

Tacícuaro (4); Tupátaro (2).

Formerly this species was abundant in the marshes around Lago de Chapala. The draining of these marshes probably resulted in reducing the numbers of these rattlesnakes. The species is known only from the Mexican Plateau at elevations of 1450 to 2400 meters.

Crotalus pusillus Klauber

Crotalus pusillus Klauber, Bull. Zool. Soc. San Diego, 26:34, August 8, 1952.—Tancítaro, Michoacán, México.

Acuaro de las Lleguas (2); Carapan; Cerro Tancítaro (16); Dos Aguas (12).

Aside from the type series of *Crotalus pusillus* from Cerro Tancítaro and one specimen from Carapan referred to the species by Klauber (1952:38), there are fourteen specimens from the Sierra de Coalcomán. These specimens (UMMZ 112566-7, 118591-9, 118601, 121512-3) are like *Crotalus pusillus* from Cerro Tancítaro in having the prefrontals paired, a black proximal rattle, and the underside of the tail black. The prefrontals are bordered posteriorly by one scale in two specimens, by two scales in three specimens, and by three scales in the other nine. The snakes from the Sierra de Coalcomán have 40 to 46 (42) dorsal body blotches. Ten males have 150-158 (154.4) ventrals and 29-33 (31.0) caudals; two females have 157 and 160 ventrals, and 25 and 27 caudals. The largest specimen is a male having a body length of 545 mm. and a tail length of 63 mm. The only noticeable difference between the specimens from the Sierra de Coalcomán and the topotypic series is that the latter have fewer dorsal blotches; the range of variation is 33 to 46 (39.8).

Most specimens of this species have a grayish brown dorsum and dark brown dorsal blotches. Two specimens from Dos Aguas (UMMZ 118596 and 118599) are pale brown above and have indistinct blotches.

One specimen from Dos Aguas regurgitated a large *Gerrhonotus imbricatus imbricatus;* of two others from the same locality, one regurgitated a *Sceloporus bulleri* and an *Eptesicus fuscus.* The latter specimen was collected at the entrance of a small cave, where it probably had captured the bat.

In the Cordillera Volcánica *Crotalus pusillus* has been obtained

in pine-oak forest at elevations between 1550 and 1800 meters. In the Sierra de Coalcomán two specimens were taken in pine forest at an elevation of 2300 meters; ten other were found beneath rocks and logs in pine-oak forest at an elevation of 2100 meters.

Crotalus triseriatus aquilus Klauber

Crotalus triseriatus aquilus Klauber, Bull. Zool. Soc. San Diego, 26:24, August 8, 1952.—Alvarez, San Luis Potosí, México.

Morelia (10); Tacícuaro (2).

I am following Klauber (1952) in assigning some of the specimens of this species from Michoacán to the subspecies *aquilus* and others to *C. t. triseriatus*. The distinguishing characters of these subspecies are given by Klauber (1952:28). On the basis of the few localities from which the species is known in Michoacán it seems as though *C. t. aquilus* inhabits the open grassy areas on the Mexican Plateau and the associated open pine-oak or oak-bunch grass habitats to the north and east of the Cordillera Volcánica. *Crotalus triseriatus aquilus* has been collected at elevations from 1600 to 2000 meters in Michoacán.

Crotalus triseriatus triseriatus (Wagler)

Uropsophus triseriatus Wagler, Natürliches System der Amphibien, p. 176, 1830.—México. (Probably Mexico City.)

Crotalus triseriatus triseriatus, Klauber, Bull. Zool. Soc. San Diego, 26:19, August 8, 1952.

Cerro Tancítaro (36); Opopeo; Pátzcuaro.

This small rattlesnake inhabits rocky areas in pine and pine-oak forests above 1600 meters in the Cordillera Volcánica; it has been collected at 3270 meters on Cerro Tancítaro. The series reported by Schmidt and Shannon (1947:84) is a mixture of specimens of *Crotalus triseriatus* and *Crotalus pusillus*. The two species are found together on Cerro Tancítaro, but only *Crotalus pusillus* inhabits the coniferous forests of the Sierra de Coalcomán. Klauber (1952:30) stated that despite the proximity of *Crotalus triseriatus triseriatus* and *Crotalus triseriatus aquilus* in Michoacán, there is no evidence of intergradation. He went on to suggest that additional material might show that the two named populations actually are distinct species. The specimens that have been studied since Klauber's investigations also show no evidence of intergradation, but there still is no known sympatry of the populations.

The small montane rattlesnakes belonging to the species *C. pricei*, *C. pusillus*, and *C. triseriatus* present a problem in systematics and distribution worthy of intensive investigation. A knowledge of the

distribution and relationships of the various populations of these snakes, together with other species also living in isolated populations on the higher mountains in México, probably will be of great significance in understanding dispersal and differentiation of animals during the Pleistocene.

SPECIES OF QUESTIONABLE OCCURRENCE

Some species for which there are no authentic records from Michoacán can be expected there on zoogeographic probability. Other species have been recorded from Michoacán, but these records are doubtful for any one of several reasons. Fifteen species of such questionable occurrence are discussed below:

Syrrhophus modestus modestus Taylor

Syrrhophus modestus Taylor, Univ. Kansas Sci. Bull., 28:304, May 15, 1942. —Hacienda Paso del Río, Colima, México.

Syrrhophus modestus modestus, Duellman, Occ. Pap. Mus. Zool. Univ. Michigan, 594:5, June 6, 1958.

This small terrestrial frog is not uncommon on the coastal lowlands and foothills in Nayarit and in Colima, where it has been collected within a few kilometers of the Michoacán border. At Tecolapa, Colima, on August 9, 1956, *Syrrhophus modestus modestus* was found with *Tomodactylus nitidus orarius, Bufo marinus, Bufo marmoreus, Hyla baudini, Hyla smithi,* and *Phyllomedusa dacnicolor,* all of which occur on the coastal lowlands of Michoacán. Because of its solitary and secretive habits, *Syrrhophus modestus modestus* is not common in collections. Additional field work on the coast of Michoacán should reveal the presence of the species there.

Hyla microcephala sartori Smith

Hyla microcephala sartori Smith, Herpetologica, 7:186, December 31, 1951.—1 mi. N of Organos, S of El Triente, Guerrero, México.

On August 28, 1960, J. R. Dixon obtained a series of this species from a temporary pond 6 kilometers northeast of La Resolana, Jalisco. Previously, *Hyla microcephala sartori* had been known only from the lowlands of Guerrero and Oaxaca. The existence of the species in Jalisco provides evidence that this frog also occurs in Michoacán and Colima.

Gastrophryne usta usta (Cope)

Engystoma ustum Cope, Proc. Acad. Nat. Sci. Philadephia, 18:131, 1866. —Guadalajara, Jalisco, México.

Gastrophryne usta usta, Carvalho, Occ. Pap. Mus. Zool. Univ. Michigan, 555:13, July 16, 1954.

Smith and Taylor (1948:93-4) listed specimens of this species from Organos and El Treinta, Guerrero, and from Paso del Río,

Quesería, Santiago, and Tecomán, Colima. The species occurs from Sinaloa and central Veracruz southward at low elevations to the Isthmus of Tehuantepec and thence along the Pacific lowlands into Central America. Almost certainly it occurs on the coastal lowlands in Michoacán. Since the amphibian fauna of the Tepalcatepec Valley has been better sampled than that of the coast, I suspect that if *Gastrophryne* occurred in the Tepalcatepec Valley, I would have found it there.

Lepidochelys olivacea (Eschscholtz)

Chelonia olivacea Eschscholtz, Zool. Atlas, pt. 1, p. 2, 1829.—Manila Bay, Philippine Islands.

Lepidochelys olivacea, Girard, United States Exploring Expedition . . ., vol. 20, Herpetology, p. 435, 1858.

According to Smith and Taylor (1950b:15), this sea turtle is known from the entire Pacific coast of México; these authors reported the species from Chiapas, Oaxaca, Guerrero, Colima, and Sonora. Although the only sea turtle that I observed in Michoacán is *Chelonia mydas*, others probably do use the sheltered beaches for nesting. The scanty records of sea turtles along the Pacific coast of México indicate that *Chelonia mydas* and *Lepidochelys olivacea* are the most abundant species in that region. There are scattered records of *Dermochelys coriacea*, *Caretta caretta*, and *Eretmochelys imbricata* along the Pacific coast. The occurrence of any of these along the coast of Michoacán is probable.

Geoemyda pulcherrima pulcherrima (Gray)

Emys pulcherrima Gray, Catalogue of the Shield Reptiles in British Museum, vol. 1, p. 25.—México. Type locality restricted to Presidio de Mazatlán, Sinaloa, México, by Smith and Taylor (1950b:30).

Geoemyda pulcherrima pulcherrima, Wettstein, Sitzb. Akad. Wiss. Wien, 143:18, 1934.

Smith and Taylor (1950b:30) recorded this species from Sonora, Sinaloa, Nayarit, Colima, and Guerrero; these records indicate that the species probably is distributed along the Pacific coast of México southward from southern Sonora. It unquestionably occurs on the coast of Michoacán. Natives of the coastal lowlands tell of another "tortuga de la tierra" besides *Geoemyda rubida*. In the collections of the Museum of Natural History of the University of Illinois is a specimen of *Geoemyda pulcherrima* from Mexcala in the Balsas Basin in northern Guerrero. On the basis of this specimen it is highly probable that the species also inhabits the Balsas-Tepalcatepec Basin in Michoacán.

Pseudemys scripta ornata (Gray)

Emys ornata Gray, Synopsis reptilium, p. 30, 1831.—Mazatlán, Sinaloa, México.

Pseudemys scripta ornata, Carr, Herpetologica, 1:135, December 30, 1938.

The systematics and distribution of *Pseudemys scripta* in México and Central America are poorly understood. Smith and Taylor (1950b:32) recorded this turtle from the Pacific lowlands of Sinaloa, Jalisco, Oaxaca, and Chiapas. This species is represented by vicarious populations throughout the Atlantic lowlands of México, northwestern México, over much of the United States, and also in Baja California. Along the Pacific coast of México the species seems to be extremely rare, or, at least, only locally abundant. Since the species has such a wide distribution, and since it occurs on the Pacific lowlands both to the north and to the south of Michoacán, it is reasonable to expect its presence on the coast of Michoacán. Inquiries among the natives living in the Balsas-Tepalcatepec Basin produced only negative evidence about the occurrence of *Pseudemys* in the Río Tepalcatepec and Río Balsas. I suspect that the best place to search for these turtles on the coast of Michoacán is in the numerous fresh-water lagoons on the coastal plain.

Caiman crocodilus fuscus (Cope)

Perosuchus fuscus Cope, Proc. Acad. Nat. Sci. Philadelphia, 20:203, November 9, 1868.—Río Magdalena, Columbia.

Caiman crocodilus fuscus, Mertens, Senckenbergiana, 26:275, December 22, 1943.

Gadow (1930:50) reported that *Caiman sclerops* (= *Caiman crocodilus fuscus*) inhabited the "tierra caliente" in Michoacán. Smith and Taylor (1950b:212) accepted Gadow's record for the State, although otherwise the species is unknown north of Oaxaca. Peters (1954:10) refuted Gadow's record on the basis that Gadow's collections contained no specimens of *Caiman*. The local name "caiman" refers to both *Crocodylus* and to *Caiman*, for, in general, the natives do not distinguish between the two. "Caimanes" are reported from along the coast of Michoacán, where the name presumably refers to *Crocodylus acutus acutus*, and in the Balsas-Tepalcatepec Basin (Gadow, 1930:50; Webber, 1946:267). I have seen no specimens of either *Crocodylus* or *Caiman* from the Balsas Basin. If crocodilians do occur in the basin, they probably are *Crocodylus acutus acutus*. There is no basis, whatsoever, for including Michoacán in the range of *Caiman crocodilus fuscus*.

Bipes canaliculatus Bonnaterre

Bipes canaliculatus Bonnaterre, Encyclopédie méthodique, Erpétologie, p. 68, 1789.—México. Type locality restricted to Mexcala, Guerrero, México, by Smith and Taylor (1950b:39).

Dugès (1896:480) reported this species from Morelia, Michoacán. Smith and Taylor (1950b:39), who recorded the species from three localities in the Balsas Basin in Guerrero, rejected Dugès' record. I, too, am unwilling to accept Dugès' record. Nevertheless, the species probably occurs throughout much of the Balsas Basin. This idea is strengthened by comments made by Storm (1939:342): "The last hard drop, that afternoon, was down the great Cerro de los Cajones [southwest of Tacámbaro], and here in the upper forest we came upon . . . a lizard with front legs and none behind . . . the animal with hands and no feet that señor Smith [Hobart M. Smith] was seeking! . . . They're named *Bipes caniculatus* (*sic.*)."

Coleonyx elegans nemoralis Klauber

Coleonyx elegans nemoralis Klauber, Trans. San Diego Soc. Nat. Hist., 10: 195, March 9, 1949.—Paso del Río, Colima, México.

Klauber (1945:199) and Smith and Taylor (1950b:43) reported this lizard from the coastal lowlands of Colima and Guerrero. Davis and Smith (1953:101) reported it from 8 kilometers northeast of Temilpa, Morelos, in the upper Balsas Basin. Specimens of this lizard have been collected infrequently; the few locality records and limited ecological data indicate that it inhabits dense scrub forest and tropical semi-deciduous forest. *Coleonyx elegans nemoralis* is to be expected on the coastal lowlands, the seaward foothills of the Sierra de Coalcomán, and on the lower slopes of the Cordillera Volcánica along the northern edge of the Tepalcatepec Valley.

Phrynosoma orbiculare orbiculare (Linnaeus)

Lacerta obricularis Linnaeus, Systema naturae, ed. 12, 1:1062, 1789.—México (by inference). Type locality restricted to México, Districto Federal, by Smith and Taylor (1950b:97).

Phrynosoma orbiculare orbiculare, Smith, Trans. Kansas Acad. Sci., 37:290, 1934.

Gadow (1905:213) inferred that *Phrynosoma orbiculare* occurred at elevations of more than 3000 feet in Michoacán. There are no specimens of this species known from Gadow's collections made in Michoacán. Smith and Taylor (1950b:98) apparently accepted Gadow's statement and recorded the species from Michoacán: "above 3000 feet (Jorullo?)." Reeve (1952:940) somehow misconstrued this statement to read "Jorullo, above Zumpango (Smith and

Taylor, 1950b)." Reeve did not indicate on his map (1952:939) that the species occurred in Michoacán. In the most recent review of the species (Horowitz, 1955), no localities are given in Michoacán. Since *Phrynosoma orbiculare* is known from central Jalisco, Guanajuato, Queretaro, and México, its presence at least in northeastern Michoacán is to be expected, although at the present time there are no specimens known from the state.

Eumeces brevirostris (Günther)

Mabouia brevirostris Günther, Proc. Zool. Soc. London, p. 316, August, 1860.—Oaxaca. Type locality restricted to Oaxaca, Oaxaca, México, by Smith and Taylor (1950b:168).

Eumeces brevirostris, Bocourt, Mission scientifique au Mexique et dans l'Amerique Centrale. Reptiles, livr. 6, p. 439, 1879.

Smith and Taylor (1950b:168) listed this species: "*Michoacán:* No specific record." I am unaware of any specimen of this skink from the state. As presently recognized, this species contains two subspecies. One of these occurs in the mountains of Oaxaca northward into central Veracruz; the other, *Eumeces brevirostris bilineatus*, occurs in Durango southward to Jalisco, where it inhabits the Sierra Madre Occidental. Possibly the species occurs in the Sierra de los Tarascos in Michoacán.

Eumeces callicephalus Bocourt

Eumeces callacephalus Bocourt, Mission scientifique au Mexique et dans l'Amerique Centrale. Reptiles, livr. 6, p. 431, 1879.—Guanajuato, Guanajuato, México.

Dugès (1896) in a paper in which he listed several species of *Eumeces* in México, reported *Eumeces callicephalus* from Michoacán, but he gave no specific locality within the state. Michoacán was included in the range of the species by Taylor (1936:298) and by Smith and Taylor (1950b:164). The species definitely is known from southeastern Arizona southward to Guanajuato. It may occur in Michoacán, but, since there are three rather widespread species of *Eumeces* inhabiting the Mexican Plateau and associated mountain ranges in the northern and northeastern part of Michoacán, interspecific competition might be a reason for the absence of *Eumeces callicephalus* there.

Leptodeira septentrionalis polysticta Günther

Leptodeira polysticta Günther, Biologia Centrali-Americana, Reptilia, p. 172, May, 1895.—Belice, British Honduras.

Leptodeira septentrionalis polysticta, Duellman, Bull. Amer. Mus. Nat. Hist., 114:72, February 24, 1958.

Although this species occurs from sea level to elevations of about 2000 meters from Nayarit southward into Central America, no

specimens are known from Michoacán. Smith and Taylor (1945: 87) listed the species as occurring in Michoacán, but they had no record on which to base this report. Probably, the species occurs on the coastal lowlands and seaward slopes of the Sierra de Coalcomán.

Tropidodipsas fasciata guerreroensis Taylor

Tropidodipsas guerreroensis Taylor, Univ. Kansas Sci. Bull., 26:470; November 27, 1940.—Buena Vista, Guerrero, México.

Tropidodipsas fasciata guerreroensis, Alvarez del Toro and Smith, Herpetologica, 12:16, March 6, 1956.

Dugès (1896:480) reported a snake, questionably of this species, from Uruapan, Michoacán. Taylor (1940c) suggested that on geographic grounds Dugès' record might refer to *T. f. guerreroensis*, which is known definitely only from the type locality. *Tropidodipsas occidentala* is known from Comala, Colima, and Coalcomán, Michoacán. On zoogeopraphic grounds that species might be found at Uruapan. Since the specimen apparently no longer is extant, the identification cannot be ascertained.

Micrurus fitzingeri fitzingeri (Jan)

Elaps fitzingeri Jan, Rev. Mag. Zool., p. 521, 1858.—México. Type locality restricted to Guanajuato, Guanajuato, México, by Smith and Taylor (1950a:330).

Micrurus fitzingeri fitzingeri, Brown and Smith, Proc. Biol. Soc. Washington, 55:63, June 25, 1942.

Smith and Taylor (1945:174) recorded the species from Zamora, Michoacán. Hobart M. Smith (*in litt.*) stated that this record was based on a report of *Elaps fulvius* from Zamora by Dugès (1896: 482). Smith guessed that the report was based on a specimen of *Micrurus fitzingeri*. The specimen has not been seen. Although the species is known from Guanajuato and México, until a specimen is available from Michoacán, the species should not be considered part of the herpetofauna of Michoacán.

GAZETTEER

The localities in Michoacán here listed are those from which specimens were examined as well as other localities mentioned in the text. The localities are arranged alphabetically according to the most definitive word or words in the total name. For example, Lago de Chapala is listed as "Chapala (Lago de)" and Cerro de Tancítaro is listed as "Tancítaro (Cerro de)." Insofar as has been possible, the following information is given for each locality: geographical co-ordinates to the nearest minute of north latitude and west longitude, elevation in meters above mean sea level, a descrip-

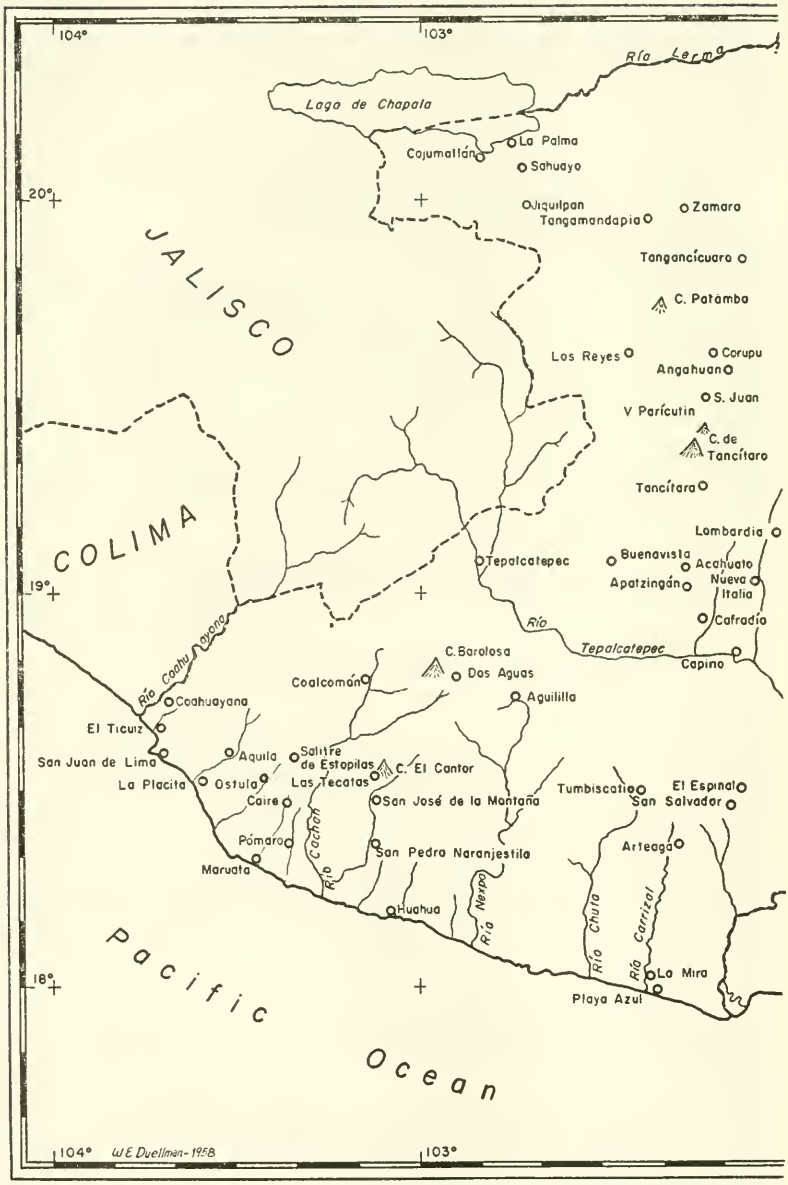


FIG. 11. Map of Michoacán showing important localities mentioned in text.

Localities not on this map can be located by directions given in the gazetteer.

tion of its geographical location, type of dominant vegetation, and in some cases comments concerning collecting sites in the vicinity. Distances are in kilometers; all are map (air line) distances, unless otherwise indicated. Many localities visited on mule trips are given as being a certain number of "mule hours" in a general direction from another town or village. In order to reach most of these localities today, one would have to go by mule, and this is the way the muleteers determine their distances. Some of the elevations are taken from maps, but most of them were obtained from one or more readings of altimeters that we carried in the field. The terms used for describing the vegetation are those defined in the section of the natural landscape.

My primary cartographic sources have been: the provisional edition of maps published by the American Geographic Society (Colima, Guadalajara, México, and San Luis Potosí sheets published between 1933 and 1940), scale 1:1,000,000; the preliminary sheets (Colima, Guadalajara, Guanajuato, and México) published in 1949 with a scale of 1:500,000 of the Carta Geográfica de la República Méxicana (Dirección de Geografía y Meterología, Secretaria de Agricultura y Ganadería); and the Carta de Cuenca Tepalcatepec (Scale 1:250,000) prepared in 1958 by the Comisión del Tepalcatepec, Secretaría de Recursos Hidráulicos. I have visited most of the 181 localities and have gathered data pertaining to vegetation, altitude, and location. I think, nevertheless, that the accuracy of some of the locations and elevations as given in the gazetteer is questionable. This situation can be rectified only by detailed geographic studies.

Most of the important towns, villages, rivers, and high mountains are shown on the accompanying map (Fig. 11). Places not shown on this map can be located from directions given in the gazetteer.

Acahuata.—Lat. 19° 10′, long. 102° 21′, elev. 1040 m. A village north of Apatzingán and on the southern slope of Cerro de Tancítaro; transition between arid tropical scrub forest and pine-oak forest; tropical semi-deciduous forest in barrancas.

Agua Cerca.—Lat. 19° 06′, long. 101° 45′, elev. 1550 m. A ranch south-southwest of Ario de Rosales on the road to La Huacana; pine-oak forest.

Aguililla.—Lat. 18° 45′, long. 102° 47′, elev. 860 m.; a town in a low valley in the Sierra de Coalcomán; arid tropical scrub forest.

Álamo (El).—Lat. 19° 42′, long. 100° 55′, elev. 2300 m. A ranch 5 kilometers by road east of El Temazcal; pine-oak forest.

Angahuan.—Lat. 19° 33′, long. 102° 14′, elev. 2440 m. A Tarascan village about 27 kilometers northwest of Uruapan; pine forest. Much of the land is still covered by a deep layer of ashes from the nearby Volcán Parícutin.

Apatzingán.—Lat. 19° 06′, long. 102° 22′, elev. 335 m. The largest town in the Tepalcatepec Valley; arid tropical scrub forest.

Apiza (Boca de).—Lat. 18° 42′, long. 103° 44′, sea level. The name of the mouth of the Río Coahuayana; sandy beach and coco palms.

Apo.—Lat. 19° 25′, long. 102° 25′, elev. 2160 m. A village on the western slope of Cerro de Tancítaro; pine-oak forest.

Aquila.—Lat. 18° 32′, long. 103° 30′, elev. 150 m. A small village on the Río Aquila in the seaward foothills of the Sierra de Coalcomán; tropical semi-deciduous forest.

Araparícuaro.—Lat. 19° 22′, long. 102° 12′, elev. 1525 m. A village 19 kilometers west-southwest of Uruapan on the trail to Tancítaro; pine-oak forest.

Araro.—Lat. 19° 54′, long. 100° 50′, elev. 1830 m. A small village at the eastern end of the Lago de Cuitzeo lakebed; mesquite-grassland.

Ario de Rosales.—Lat. 19° 12′, long. 101° 42′, elev. 1980 m. A town in the Cordillera Volcánica on the road from Pátzcuaro to La Huacana; mixed hardwoods and pine forest.

Arteaga (formerly Carrizal).—Lat. 18° 28′, long. 102° 25′, elev. 850 m. A town in the eastern part of the Sierra de Coalcomán; transition between arid tropical scrub forest and oak forest.

Atzimba.—Lat. 19° 39′, long. 100° 47′, elev. 2900 m. A national park in the Cordillera Volcánica, located between Ciudad Hidalgo and Morelia, 32 kilometers by road west-southwest of Ciudad Hidalgo; mixed pine and fir forest.

Axolotl (Rancho).—Lat. 19° 47′, long. 100° 38′, elev. 2900 m. A settlement on the western slopes of Cerro San Andrés; pine, oak, and fir forest.

Balsas (Río).—A large river having its headwaters in Tlaxcala, Puebla, and northwestern Oaxaca, flowing westward through an arid valley to the Pacific Ocean, and in its lower part forming the boundary between Michoacán and Guerrero.

Barolosa (Cerro de).—Lat. 18° 52′, long. 102° 57′, elev. 2900-3050 m. Presumably the highest mountain in the Sierra de Coalcomán and located about 13 hours by mule east-northeast of Coalcomán; open pine-oak-fir forest and alder thickets.

Barolosa (Rancho).—Lat. 18° 50′, long. 103° 00′, elev. 2320 m. A small ranch on the west-northwestern slope of Cerro de Barolosa, about 11 hours by mule east-northeast of Coalcomán; open pine-oak forest.

Barranca Seca.—Lat. 19° 32′, long. 102° 15′, elev. 2100 m. A small village about 7 kilometers northwest of San Juan de Parangaricutiro; pine forest.

Bejuco (Barranca de).—Lat. 18° 07′, long. 102° 48′, elev. 90 m. A barranca in the lower slopes of the Sierra de Coalcomán just west of the lower reaches of the Río Nexpa; tropical semi-deciduous forest.

Buenavista (Tomatlán).—Lat. 19° 17′, long. 102° 36′, elev. 425 m. A village on the Río Masiaco in the Tepalcatepec Valley, 33 kilometers by road west-northwest of Apatzingán; open arid tropical scrub forest.

Buena Vista.—Lat. 18° 40′, long. 102° 09′, elev. 600 m. A ranch on the northeastern slopes of the Sierra de Coalcomán; arid tropical scrub forest.

Cachán (Río).—Lat. 18° 14′, long. 103° 14′. A river formed by the affluence of the Río Coalcomán and the Río San José and flowing into the Pacific Ocean at a point indicated by the co-ordinates given above. Sometimes the name is applied to the lower part of the river as used here; other times the name is used for the entire length of the Río Coalcomán.

Camichines.—Lat. 18° 47′, long. 103° 05′, elev. 1070 m. A ranch about 5 kilometers east-northeast of Coalcomán; transition between arid tropical scrub forest and oak forest.

Camécuaro (Lago de).—Lat. 19° 55′, long. 102° 13′, elev. 1615 m. A small lake (depth to about 10 m.) drained by the Río Duero and located one kilometer north-northwest of Tangancícuaro; mesquite-grassland and some cypress and oak around the lake.

Cancita (Río).—A tributary of the Río Tepalcatepec flowing southward from the southeastern slope of Cerro de Tancítaro.

Cantiles (Los).—Lat. 19° 43′, long. 100° 55′, elev. 2160 m. A ranch 33 kilometers by road east of Morelia; pine forest.

Capácuaro.—Lat. 19° 33′, long. 102° 02′, elev. 2070 m. A Tarascan village 18 kilometers by road north of Uruapan; pine forest.

Capirio.—Lat. 18° 52′, long. 102° 08′, elev. 180 m. A village on the Río Tepalcatepec, 22 kilometers by road south of Nueva Italia; open arid tropical scrub forest and some gallery forest along the river.

Carapan.—Lat. 19° 52′, long. 102° 02′, elev. 2070 m. A village on the northern edge of the Sierra de los Tarascos, 32 kilometers by road west of Zacapu; pine-oak forest at village and to the south; mesquite-grassland immediately to the north.

Cerrito (El).—Lat. 18° 45′, long. 103° 40′, elev. 15 m. A ranch about 3 kilometers northeast of Coahuayana; tropical semi-deciduous forest.

Chapala (Lago de).—A large lake on the Mexican Plateau at an elevation of 1525 m., partly in the state of Jalisco. It is drained by the Río Grande de Santiago, which flows northward and then westward into the Pacific Ocean. Immediately to the east of the lake are remnants of once extensive marshes.

Charapendo.—Lat. 19° 15′, long. 102° 04′, elev. 975 m. A village 24 kilometers by road south of Uruapan near the upper limit of the arid tropical scrub forest in the Tepalcatepec Valley.

Cherán.—Lat. 19° 42′, long. 101° 57′, elev. 2350 m. A Tarascan village 27 kilometers by road south-southeast of Carapan; pine forest.

Chichihuas.—Lat. 18° 47′, long. 103° 12′, elev. 1200 m. A ranch about 6 kilometers west-southwest of Coalcomán; scrub oak forest.

Chinapa.—Lat. 19° 22′, long. 100° 51′, elev. 930 m. A small village on the Río Chinapa, 43 kilometers south of El Temzcal on the road to Huetamo; arid tropical scrub forest.

Chupio.—Lat. 19° 10′, long. 101° 27′, elev. 1080 m. A village 12 kilometers by road south of Tacámbaro; transition between arid tropical scrub forest and oak forest.

Churumuco.—Lat. 18° 37′, long. 101° 38′, elev. 210 m. A small town in the Balsas Valley; arid tropical scrub forest.

Ciénega (La).—Lat. 18° 28′, long. 103° 18′, elev. 900 m. A ranch about 3 hours by mule north of Coire; tropical semi-deciduous forest.

Coahuayana.—Lat. 18° 44′, long. 103° 31′, elev. 15 m. A village on the coastal plain near the mouth of the Río Coahuayana; arid tropical scrub forest and tropical semi-deciduous forest.

Coalcomán.—Lat. 18° 47′, long. 103° 08′, elev. 945 m. The largest town in the Sierra de Coalcomán and situated in a valley about 12 by 6 kilometers; arid tropical scrub forest on valley floor; oaks and some tropical semi-deciduous forest on surrounding slopes.

Coalcomán (Río).—A river having its headwaters northeast of the town of Coalcomán and flowing southward to join with the Río San José to form the Río Cachán.

Coalcomán (Sierra de).—A highland mass outlined by the Río Coahuayana and its tributaries on the west, the Río Tepalcatepec on the north, and the Río Balsas on the east, and the Pacific Ocean on the south. The axis of the sierra extends for about 200 kilometers in a west-northwest to east-southeast direction; the mountains are nearly 80 kilometers in breadth; the highest parts of the range are about 3000 meters above sea level.

Cofradía.—Lat. 18° 56′, long. 102° 17′, elev. 215 m. A ranch about 17 kilometers southeast of Apatzingán; arid tropical scrub forest.

Coire.—Lat. 18° 26′, long. 103° 22′, elev. 300 m. A village on the seaward foothills of the Sierra de Coalcomán on the Río Coire; tropical semi-deciduous forest.

Cojumatlán.—Lat. 20° 07′, long. 102° 51′, elev. 1530 m. A village on the southeastern shore of Lago de Chapala; mesquite-grassland.

Colola (Río).—A small river emptying into the Pacific Ocean between Maruata and Punto San Telmo.

Conejos (Los).—Lat. 19° 22′, long. 102° 07′, elev. 1850 m. A village 6 kilometers west-southwest of Uruapan, and sometimes known as Nuevo San Juan; pine-oak forest.

Copándaro.—Lat. 19° 54′, long. 101° 12′, elev. 1800 m. A village on the south edge of the Lago de Cuitzeo lakebed; mesquite-grassland.

Copuyo (Capuyo or Copullo).—Lat. 18° 28′, long. 100° 56′, elev. 1200 m. A small village about 5 kilometers by road west of Paso Ancho; transition between arid tropical scrub forest and oak forest.

Cordillera Volcánica.—A mountain range along the southern edge of the Mexican Plateau, roughly along the nineteenth parallel, and made up of many volcanos; the range extends from Volcán de Colima on the west to Cofre de Perote and Orizaba in Veracruz; several of the volcanos reach elevations of more than 4000 meters.

Corralito (El).—Lat. 18° 52′, long. 102° 38′, elev. 270 m. A small village in the Tepalcatepec Valley, about 30 kilometers southwest of Apatzingán; arid tropical scrub forest.

Corupu (Corupo).—Lat. 19° 28′, long. 102° 19′, elev. 2450 m. A village 29 kilometers northwest of Uruapan; pine forest.

Cuatro Caminos.—Lat. 19° 00′, long. 102° 05′, elev. 335 m. A village 4 kilometers south of Nueva Italia; arid tropical scrub forest.

Cuilala (Playa).—Lat. 18° 10′, long. 103° 06′, sea level. A sandy beach on the Pacific Ocean just east of La Higuerita.

Cuitzeo.—Lat. 19° 58′, long. 101° 09′, 1800 m. A village on the north shore of the Lago de Cuitzeo lakebed; mesquite-grassland.

Cuitzeo (Lago de).—A large lakebed on the Mexican Plateau at an elevation of 1800 m. In dry years there is little water in the lake, and most of the lakebed is dry; in very wet years the entire lakebed is flooded. The Río de Morelia flows into the lake, which has no outlet; surrounding vegetation is mesquite-grassland.

Cuseño Station.—Lat. 19° 30′, long. 102° 16′, elev. 2200 m. A field station of the American Geological Society established in 1945 and demolished in 1953; located at the northern edge of the lava flow at Volcán Parícutin; remnants of pine forest.

Diezmo (El).—Lat. 18° 26′, long. 103° 19′ elev. 850 m. A ranch about 8 kilometers north of Coire; tropical semi-deciduous forest.

Dos Aguas.—Lat. 18° 45′, long. 102° 55′, elev. 2100 m. A lumber camp on the eastern slope of Cerro de Barolosa, located about 22 kilometers west-northwest of Aguililla; pine-oak forest and some fir forest in sheltered ravines.

Duero (Río).—A small river having its headwaters near Tangancícuaro and flowing northwestward into the Río Lerma; source of irrigation water for surrounding agricultural area.

Emiliano Zapata.—Lat. 18° 59′, long. 102° 39′, elev. 1600 m. A town 10 kilometers east of Jiquilpan; mesquite-grassland and irrigated fields.

Erongaricuaro.—Lat. 19° 35′, long. 101° 43′, elev. 2150 m. A Tarascan village on the western shore of Lago de Pátzcuaro; pine forest.

Espinal (El).—Lat. 18° 27′, long. 102° 07′, elev. 500 m. A ranch in the northern foothills of the Sierra de Coalcomán, 9 kilometers by road north-northeast of San Salvador; arid tropical scrub forest.

Estopilas (Salitre de).—Lat. 18° 30′, long. 103° 23′, elev. 130 m. A small village about 10 kilometers east of Ostula; tropical semi-deciduous forest and arid tropical scrub forest.

Garnica (Cerro).—Lat. 19° 43′, long. 100° 48′, elev. 3000 m. A mountain about 8 kilometers north of Pino Gordo; pine-oak-fir forest.

Garnica (Puerto de).—Lat. 19° 42′, long. 100° 51′, elev. 2840 m. A mountain pass 46 kilometers by road west of Ciudad Hidalgo; pine and fir forest.

Gregorio (San).—Lat. 19° 25′, long. 101° 24′, elev. 2200 m. A ranch about 16 kilometers southeast of Pátzcuaro; pine forest.

Guayabo.—Lat. 18° 45′, long. 102° 15′, elev. 760 m. A village in the Sierra de Coalcomán about 32 kilometers north-northeast of Arteaga; upper limits of arid tropical scrub forest.

Herradero (Barranca de).—Lat. 18° 17′, long. 103° 08′, elev. 200-250 m. A barranca south of San Pedro Naranjestila in the Sierra de Coalcomán; tropical semi-deciduous forest.

Hidalgo (Ciudad).—Lat. 19° 32′, long. 100° 34′, elev. 2100 m. A town in the valley of the Río Tuxpan; mesquite-grassland and pine-oak forest.

Higuerita (La).—Lat. 18° 12′, long. 103° 06′, sea level. A place name on the Pacific coast; sandy beach and arid tropical scrub forest.

Higuertas (Las).—Lat. 18° 39′, long. 103° 17′, elev. 1600 m. A ranch about 7 hours by mule southwest of Coalcomán; pine-oak forest.

Hondo (Puerto).—Lat. 19° 25′, long. 100° 13′, elev. 2750 m. A pass in the mountains, 14 kilometers by road east of Zitácuaro (just west of Macho de Agua); pine, oak, and fir forest.

Huancana (La).—Lat. 18° 58′, long. 101° 50′, elev. 550 m. A village in the Balsas Basin; arid tropical scrub forest.

Huahua (La).—Lat. 18° 12′, long. 103° 00′, sea level. A small village on the Pacific coast; arid tropical scrub forest and gallery forest along the Arroyo de Huahua.

Huetamo.—Lat. 18° 38′, long. 100° 53′, elev. 300 m. A town in the Balsas Valley; arid tropical scrub forest.

Huingo.—Lat. 19° 55′, long. 100° 50′, elev. 1800 m. A village on the eastern edge of the Lago de Cuitzeo lakebed; mesquite-grassland.

Jacona.—Lat. 19° 57′, long. 102° 18′, elev. 1600 m. A small town, 4.3 kilometers by road southwest of Zamora; mesquite-grassland.

Jaramillo.—Lat. 19° 20′, long. 102° 02′, elev. 1500 m. A ranch 9 kilometers by road south of Uruapan; pine-oak forest.

Jazmin.—Lat. 18° 52′, long. 101° 58′, elev. 275 m. A village in the Tepalcatepec Valley, 32 kilometers by road southeast of Cuatro Caminos; open arid tropical scrub forest.

Jeráhuaro.—Lat. 19° 52′, long. 100° 35′, elev. 2600 m. A town in the northern part of the state and located east of Lago de Cuitzeo; pine-oak forest.

Jiquilpan.—Lat. 19° 59′, long. 102° 43′, elev. 1570 m. A town just southeast of Lago de Chapala; mesquite-grassland.

Jorullo (Volcán).—Lat 19° 00′, long. 101° 45′, elev. 1300 m. (crest). A cinder and lava cone rising from the foothills of the Cordillera Volcánica; arid tropical scrub forest on lower slopes and pine-oak forest on top.

Jungapeo.—Lat. 19° 26′, long. 100° 29′, elev. 1430 m. A village in the valley of the Río Tuxpan, about 13 kilometers south of Tuxpan on the southern slopes of the Mexican Plateau; tropical semi-deciduous forest and pine-oak forest.

Lengua de Vaca (Puerto de).—Lat. 19° 26′, long. 100° 13′, elev. 2900 m. A pass in the mountains at the Michoacán-Mexico border through which passes the Mexico City-Morelia highway; pine and fir forest.

Lerma (Río).—A river originating in the state of México and flowing westward, and forming the northern boundary of the state of Michoacán, to Lago de Chapala.

Lima (San Juan de).—Lat. 18° 29′, long. 102° 42′, sea level. A ranch on the Pacific coast; arid tropical scrub forest and tropical semi-deciduous forest.

Lima (Punta San Juan de).—Lat. 18° 38′, long. 102° 43′, sea level. A rocky promontory jutting into the Pacific Ocean just southwest of San Juan de Lima; arid tropical scrub forest.

Limoncito.—Lat. 18° 45′, long. 102° 43′, elev. 730 m. A ranch 10 kilometers north of Aguililla; arid tropical scrub forest; tropical semi-deciduous gallery forest along the nearby Río Tepecuate.

Lombardia.—Lat. 19° 08′, long. 102° 02′, elev. 640 m. A town in the Tepalcatepec Valley, 38 kilometers by road south of Uruapan; arid tropical scrub forest.

Lleguas (Acuaro de las).—Lat. 18° 48′, long. 102° 52′, elev. 2320 m. A place name for a stream and meadow (Llano de la Llegua) surrounded by pine-oak forest, located about 10 hours by mule east of Coalcomán.

Macho de Agua.—Lat. 19° 25′, long. 100° 15′, elev. 2850 m. A ranch just west of Puerto de Lengua de Vaca and 16 kilometers by road east of Zitácuaro; mixed oak, pine, and fir forest.

Maquili.—Lat. 18° 36′, long. 103° 32′, elev. 120 m. A village on the Río Aquila about 3 kilometers south-southwest of Aguila; tropical semi-deciduous forest.

Maravatio.—Lat. 19° 53′, long. 100° 27′, elev. 2010 m. A town in the Río Lerma Valley; irrigated fields on flats and pine-oak forest on slopes.

Marquez (Río).—A tributary to the Río Tepalcatepec, flowing through a deep gorge (Barranca del Marquez) between Lombardia and Nueva Italia. The stream originates from springs near Uruapan, where the stream is known as the Río Cupatitzio.

Maruata.—Lat. 18° 17′, long. 103° 20′, sea level. Place name for a Nineteenth Century port of little importance near the mouth of the Río Coire; sandy beach, fresh-water lagoon, and arid tropical scrub forest.

Mexcala (Laguna).—Lat. 18° 29′, long. 103° 41′, sea level. A brackish lagoon surrounded by mangroves, located just southwest of El Ticuiz.

Mil Cumbres.—Lat. 19° 39′, long. 100° 47′, elev. 2800 m. A name for a lookout on the México-Morelia highway in Atzimba National Park, about 32 kilometers by road west-southwest of Ciudad Hidalgo; pine and fir forest.

Mira (La).—Lat. 18° 05′, long. 102° 20′, elev. 20 m. A small village about 5 kilometers north-northeast of Playa Azul; arid tropical scrub forest.

Morelia.—Lat. 19° 43′, long. 101° 10′, elev. 1900 m. Capital of and largest city in Michoacán; mesquite-grassland on flats and pine-oak forest on surrounding hills.

Morelia (Río de).—A small, intermittent stream originating in the mountains south of Morelia and emptying into Lago de Cuitzeo.

Motín del Oro.—Lat. 18° 14′, long. 103° 48′, sea level. A ranch on the Pacific coast; arid tropical scrub forest.

Motín (Río).—Lat. 18° 13′, long. 103° 48′ (mouth). A small river flowing from the Sierra de Coalcomán into the Pacific Ocean.

Nahuatzen (Nauhuatzin).—Lat. 19° 42′, long. 101° 50′, elev. 2450 m. A Tarascan village in the mountains west of Lago de Pátzcuaro; pine forest.

Nexpa (Río).—Lat. 18° 05′, long. 102° 47′ (mouth). A large river draining the central part of the Sierra de Coalcomán, originating near Aguililla, and flowing into the Pacific Ocean.

Nogueleras.—Lat. 18° 34′, long. 103° 17′, elev. 1600 m. A ranch about 10 hours by mule south-southwest of Coalcomán; oak forest.

Nueva Italia.—Lat. 19° 02′, long. 102° 07′, elev. 380 m. A town in the Tepalcatepec Valley, 59 kilometers by road south of Uruapan; arid tropical scrub forest.

Nuevo (Rancho).—Lat. 18° 26′, long. 102° 07′, elev. 520 m. A ranch 7 kilometers by road north-northeast of San Salvador in the northern foothills of the Sierra de Coalcomán; arid tropical scrub forest.

Ocorla.—Lat. 18° 38′, long. 103° 07′, elev. 885 m. A ranch about 6 hours by mule south-southeast of Coalcomán; scrubby oak forest.

Opopeo.—Lat. 19° 24′, long. 101° 37′, elev. 2800 m. A village 16 kilometers south of Pátzcuaro; pine and fir forest.

Orilla (La).—Lat. 18° 00′, long. 102° 12′, elev. 10 m. The site of a former hacienda of the same name near the mouth of the Río Balsas; arid tropical scrub forest.

Oropeo.—Lat. 18° 52′, long. 101° 48′, elev. 300 m. A village in the Tepalcatepec Valley about 13 kilometers south of La Huacana; arid tropical scrub forest.

Ostula.—Lat. 18° 30′, long. 103° 28′, elev. 120 m. A village in the seaward foothills of the Sierra de Coalcomán, located on the Río Ostula about 16 kilometers east-southeast of La Placita; arid tropical scrub forest and scattered tropical semi-deciduous forest.

Ozumatlán (Sierra de).—A range in the Cordillera Volcánica extending east-northeast from a point south of Morelia to Queréndaro and reaching elevations in excess of 2600 m.

Palma (La).—Lat. 20° 09′, long. 102° 46′, elev. 1525 m. A village on the southeastern shore of Lago de Chapala; lake-shore marshes and mesquite-grassland.

Paracho.—Lat. 19° 39′, long. 102° 02′, elev. 2375 m. A Tarascan village in the Cordillera Volcánica, located 35 kilometers by road north of Uruapan; pine forest.

Parangaricutiro (San Juan de).—Lat. 19° 30′, long. 102° 15′, elev. 2200 m. A former Tarascan village that was destroyed by the eruption of Volcán Parícutin; lava and volcanic ash amidst open pine forest.

Parícutin (Volcán).—Lat. 19° 30′, long. 102° 16′, elev. 2200 m. at base and 2700 m. at summit. A volcano born in February, 1943; it ceased to be active in December, 1951, and is located at the north-northeastern base of Cerro de Tancítaro; volcanic ash and lava amidst open pine forest.

Paso Ancho.—Lat. 19° 28′, long. 100° 52′, elev. 1100 m. A small village 30 kilometers south of El Temazcal on the road to Huetamo; arid tropical scrub forest.

Patamba (Sierra).—Lat. 19° 45′, long. 102° 21′, elev. 3700 m. at summit. A mountain, the summit of which is about 22 kilometers southwest of Tangancícuaro; pine forest from 2000 to 2600 m.; fir forest above 2600 m.

Pátzcuaro.—Lat. 19° 30′, long. 101° 36′, elev. 2200 m. A town near the southeastern shore of Lago de Pátzcuaro; pine forest.

Pátzcuaro (Lago de).—A large lake on the southwestern part of the Mexican Plateau at an elevation of 2165 m. It has no outlet. The lake is surrounded by mountains supporting pine and pine-oak forest. Along the southern and eastern shores of the lake are small marshes.

Peñas (Las).—Lat. 18° 03′, long. 102° 38′, sea level. A small village on the Pacific coast; arid tropical scrub forest.

Pichi (Estero).—Lat. 18° 01′, long. 102° 24′, sea level. A brackish lagoon surrounded by mangroves and coconut groves, located just east of Playa Azul.

Pino Gordo.—Lat. 19° 42′, long. 100° 45′, elev. 2600 m. A ranch 37 kilometers by road west of Ciudad Hidalgo; pine-oak forest.

Placita (La).—Lat. 18° 32′, long. 103° 37′, elev. 20 m. A village on the coastal lowlands, located on the Río Aquila; arid tropical scrub forest; tropical semi-deciduous forest along the river.

Playa (La).—Lat. 18° 57′, long. 102° 33′, elev. 800 m. A small village on the western edge of the lava flow of Volcán Jorullo; arid tropical scrub forest and some tropical semi-deciduous forest in ravines.

Playa Azul.—Lat. 18° 01′, long. 102° 25′, sea level. A village on the Pacific coast near the mouth of the Río Carrizal; arid tropical scrub forest; coconut plantations; mangrove-lined lagoons.

Pómaro.—Lat. 18° 18′, long. 103° 17′, elev. 300 m. An Indian village in the southern foothills of the Sierra de Coalcomán, located about 3 hours by mule north-northeast of Maruata; tropical semi-deciduous forest.

Pozos (Los).—Lat. 18° 30′, long. 103° 17′, elev. 300 m. A ranch located about 5 hours by mule north of Coire; tropical semi-deciduous forest.

Queréndaro.—Lat. 19° 48′, long. 100° 53′, elev. 1900 m. A town on the Mexican Plateau south of Lago de Cuitzeo; mesquite-grassland.

Quiroga.—Lat. 19° 42′, long. 101° 30′, elev. 2200 m. A Tarascan town on the north edge of Lago de Pátzcuaro; mesquite-grassland and pine-oak forest.

Reyes (Los).—Lat. 19° 35′, long. 102° 28′, elev. 1500 m. A town in western Michoacán, 50 kilometers south-southwest of Zamora; mesquite-grassland, oak and pine forest.

Sabino (El).—Lat. 19° 14′, long. 102° 03′, elev. 1050 m. A hacienda about 24 kilometers south of Uruapan; arid tropical scrub forest, many streams, rice fields.

Sahuayo.—Lat. 20° 05′, long. 102° 43′, elev. 1550 m. A town just south of the eastern end of Lago de Chapala; mesquite-grassland.

Salada (La).—Lat. 19° 07′, long. 102° 00′, elev. 580 m. A ranch southwest of Lombardia; arid tropical scrub forest.

Salto (Arroyo El).—Lat. 18° 45′, long. 103° 04′, elev. 1370 m. A valley of the Río Flores about 3 hours by mule east-southeast of Coalcomán; pine-oak forest.

San Andrés (Cerro).—Lat. 19° 48′, long. 100° 35′, elev. 3950 m. at summit. A mountain, the summit of which is about 16 kilometers north-northwest of Ciudad Hidalgo; oak forest to 2500 m. and pine and fir forest above 2500 m.

San José (de la Cumbre).—Lat. 19° 41′, long. 100° 50′, elev. 2750 m. A ranch 51 kilometers by road east of Morelia; pine and fir forest.

San José (de la Montaña).—Lat. 18° 25′, long. 103° 06′, elev. 750 m. A village sometimes called La Guitarra, located 14 hours by mule south-southeast of Coalcomán; tropical semi-deciduous forest.

San Pedro Naranjestila.—Lat. 18° 17′, long. 103° 06′, elev. 500 m. An Indian village in the southern foothills of the Sierra de Coalcomán; tropical semi-deciduous forest.

San Salvador.—Lat. 18° 25′, long. 102° 08′, elev. 700 m. A small village in the Sierra de Coalcomán, 37 kilometers by road northeast of Arteaga; arid tropical scrub forest.

San Telmo (Ojos de Agua de).—Lat. 18° 37′, long. 103° 42′, sea level. A small settlement at the base of Punto San Juan de Lima; tropical semi-deciduous forest and groves of oil palms.

San Telmo (Punta).—Lat. 18° 18′, long. 103° 29′, sea level. A rocky promontory jutting into the Pacific Ocean, on which there is a lighthouse (El Faro); arid tropical scrub forest.

Santa Ana.—Lat. 18° 27′, long. 102° 06′, elev. 600 m. A ranch about 4 kilometers by road northeast of San Salvador; arid tropical scrub forest.

Tacámbaro.—Lat. 19° 05′, long. 101° 22′, elev. 1820 m. A town in the Cordillera Volcánica; pine forest.

Tacícuaro.—Lat. 19° 38′, long. 101° 18′, elev. 2000 m. A village 21 kilometers east-southeast of Quiroga; mesquite-grassland and scrubby oak forest.

Tafétan.—Lat. 19° 43′, long. 100° 52′, elev. 1000 m. A village 40 kilometers by road south of El Temazcal; arid tropical scrub forest.

Tancítaro.—Lat. 19° 20′, long. 102° 22′, elev. 1850 m. A small town on the southern slope of Cerro de Tancítaro; pine-oak forest.

Tancítaro (Cerro de).—Lat. 19° 25′, long. 102° 18′, elev. 3870 m. at summit. An old volcano in the Cordillera Volcánica; the southern slope drops into the Tepalcatepec Valley; the summit is about 30 kilometers west of Uruapan; pine and oak forest on lower slopes replaced by pine or fir forest above.

Tangamandapio.—Lat. 19° 56′, long. 102° 25′, elev. 1700 m. A small town on the Mexican Plateau between Jiquilpan and Zamora; mesquite-grassland and irrigated fields.

Tangancícuaro.—Lat. 19° 52,′ long. 102° 13′, elev. 1770 m. A town 12 kilometers by road southeast of Zamora; mesquite-grassland and irrigated fields.

Tarascos (Sierra de los).—A name applied to that part of the Cordillera Volcánica extending eastward from Cerro de Tancítaro and Sierra Patamba to Pátzcuaro.

Tarécuaro.—Lat. 19° 53′, long. 102° 29′, elev. 1700 m. A village on the Mexican Plateau, 26 kilometers southwest of Zamora; mesquite-grassland and pine-oak forest.

Tecatas (Las).—Lat. 18° 36′, long. 103° 17′, elev. 1950 m. A ranch located about 10 hours by mule south-southwest of Coalcomán; oak forest.

Temazcal (El).—Lat. 19° 40′, long. 100° 56′, elev. 2200 m. A road junction, 29 kilometers east of Morelia; here the road to Huetamo leads south from the Mexico City-Morelia highway; pine forest.

Tepalcatepec.—Lat. 19° 10′, long. 102° 50′, elev. 570 m. A village in the upper Tepalcatepec Valley; arid tropical scrub forest.

Tepalcatepec (Río).—A large river having its headwaters in southeastern Jalisco and flowing through a broad valley, which separates the Cordillera Volcánica from the Sierra de Coalcomán, to the Río Balsas.

Ticuiz (El).—Lat. 18° 40′, long. 103° 40′, elev. 10 m. A village on the coastal plain about 11 kilometers south of Coahuayana; arid tropical scrub forest and tropical semi-deciduous forest.

Tinguidín.—Lat. 19° 45′, long. 102° 28′, elev. 1800 m. A small town, 17 kilometers north of Los Reyes; pine-oak forest.

Tizupan (Río).—Lat. 18° 09′, long. 102° 55′ (mouth). A small river flowing southward from the Sierra de Coalcomán to the Pacific Ocean.

Tlalpujahua.—Lat. 19° 48′, long. 100° 10′, elev. 2600 m. A mining town in the northeastern part of the state; pine and fir forest.

Tumbiscatio.—Lat. 18° 32′, long. 102° 20′, elev. 900 m. A town in the Sierra de Coalcomán; arid tropical scrub forest.

Tupátaro.—Lat. 19° 53′, long. 100° 15′, elev. 2050 m. A village in the northeastern corner of the state, 13 kilometers northwest of Tlalpujahua; oak forest.

Tuxpan.—Lat. 19° 35′, long. 100° 27′, elev. 1850 m. A town in a basin nearly surrounded by mountains and near the headwaters of the Río Tuxpan, 19 kilometers by road east-southeast of Ciudad Hidalgo; arid mesquite-grassland and irrigated fields.

Tuxpan (Río).—A river draining the mountains in the eastern part of the state and flowing southward into the Río Balsas.

Tzararacua (Cascada).—Lat. 19° 18′, long. 102° 02′, 1430 m. A waterfalls of the Río Cupatitzio, 10.5 kilometers by road south of Uruapan; oak forest with scattered pines.

Tzintzuntzan.—Lat. 19° 38′, long. 101° 35′, elev. 2170 m. A village at the site of the seat of the ancient Tarascan empire on the eastern shore of Lago de Pátzcuaro; grasslands and marshes.

Tzitzio.—Lat. 19° 35′, long. 100° 55′, elev. 1630 m. A village 16 kilometers by road south of El Temazcal; pine-oak and arid tropical scrub forest.

Ucareo (Serranía de).—A part of the Cordillera Volcánica, including Cerro San Andrés.

Undameo.—Lat. 19° 34′, long. 101° 17′, elev. 2000 m. A village 20 kilometers west-southwest of Morelia; mesquite-grassland.

Uruapan.—Lat. 19° 25′, long. 102° 02′, elev. 1630 m. A large town on the southern slopes of the Cordillera Volcánica; pine-oak forest.

Zacapu.—Lat. 19° 48′, long. 101° 47′, elev. 2000 m. A town on the Mexican Plateau; mesquite-grassland.

Zamora.—Lat. 19° 59′, long. 102° 17′, elev. 1570 m. A large town on the Mexican Plateau; mesquite-grassland.

Zicuiran.—Lat. 18° 53′, long. 101° 55′, elev. 190 m. A small village 23 kilometers east-southeast of Cuatro Caminos; arid tropical scrub forest.

Zinapécuaro.—Lat. 19° 52′, long. 100° 49′, elev. 1900 m. A town near the southeastern end of Lago de Cuitzeo; mesquite-grassland and pine-oak forest.

Ziracuaretiro.—Lat. 19° 25′, long. 101° 52′, elev. 1230 m. A village 19 kilometers by road east of Uruapan; transition between pine-oak forest and arid tropical scrub forest.

Zirimícuaro.—Lat. 19° 24′, long. 101° 56′, elev. 1300 m. A hacienda 13 kilometers by road east of Uruapan; pine-oak forest and fields of sugar cane.

Zitácuaro.—Lat. 19° 25′, long. 100° 21′, elev. 2100 m. A town in the highlands of eastern Michoacán; pine-oak forest.

Zurumbeneo.—Lat. 19° 43′, long. 101° 02′, elev. 2100 m. A ranch 19 kilometers by road east of Morelia; scrubby oak forest.

SUMMARY

The preceding analysis of the amphibians and reptiles of the state of Michoacán shows that the herpetofauna is composed of 176 species and subspecies definitely recorded from the state, plus ten others that probably occur there. Ten species are reported for the first time from Michoacán: *Pseudoeurycea robertsi, Leptodactylus occidentalis, Microbatrachylus pygmaeus, Pternohyla fodiens, Hypopachus caprimimus, Phyllodactylus homolepidurus, Anolis dunni, Sceloporus bulleri, Sceloporus heterolepis,* and *Geagras redimitus.* Five species that have been reported previously from Michoacán are based on specimens having unreliable locality data or on misidentifications; therefore, the following species are not considered to be a part of the herpetofauna of Michoacán: *Caiman crocodilus fuscus, Urosaurus irregularis, Geophis nasalis, Tropidodipsas fasciata guerreroensis,* and *Micrurus fitzingeri fitzingeri.*

Systematic studies based at least in part on specimens from Michoacán have resulted in a redefinition of nine species and subspecies: *Bufo marmoreus, Bufo perplexus, Anolis nebulosus, Anolis nebuloides, Sceloporus bulleri, Sceloporus heterolepis, Sceloporus melanorhinus calligaster, Hypsiglena torquata torquata,* and *Hypsiglena torquata ochrorhyncha.*

Nine species that previously have been recognized as valid have been placed in synonymy. These are: *Bufo horribilis* Wiegmann, 1833, and *Bufo angustipes* Smith and Taylor, 1945, as synonyms of

Bufo marinus (Linnaeus), 1758. *Microbatrachylus albolabris* Taylor, 1940, *Microbatrachylus minimus* Taylor, 1940, and *Microbatrachylus imitator* Taylor, 1942, as synonyms of *Microbatrachylus pygmaeus* (Taylor), 1937. *Phrynohyas corasterias* Shannon and Humphrey, 1957, as a synonym of *Phrynohyas inflata* (Taylor), 1944. *Hyla microeximia* Maslin, 1957, as a synonym of *Hyla eximia* Baird, 1854. *Hylella azteca* Taylor, 1943, as a synonym of *Hyla smaragdina* Taylor, 1940. *Loxocemus sumichrasti* Bocourt, 1876, as a synonym of *Loxocemus bicolor* Cope, 1861. *Eleutherodactylus vocalis* Taylor, 1940, is considered to be a subspecies of *Eleutherodactylus rugulosus*. The populations of *Thamnophis dorsalis* in the Tepalcatepec Valley are shown to be distinct from those inhabiting the highlands of the state; *Thamnophis dorsalis postremus* Smith, 1942, is revived for the population in the Tepalcatepec Valley.

Descriptions are given of the tadpoles of *Bufo occidentalis* and *Hyla bistincta*.

LITERATURE CITED

Anderson, J. D.
1960. *Storeria storerioides* in western Mexico. Herpetologica, 16:63-6, March 31.

Bogert, C. M., and Oliver, J. A.
1945. A preliminary analysis of the herpetofauna of Sonora. Bull. Amer. Mus. Nat. Hist., 83:297-426, March 30.

Boulenger, G. A.
1885. Catalogue of the lizards in the British Museum, vol. II. London, xiii + 497 pp., November 15.

1894. Catalogue of the snakes in the British Museum, vol. II, London, xi + 382 pp., September 23.

Conant, R.
1953. Three new water snakes of the genus *Natrix* from Mexico. Nat. Hist. Misc., 126:1-9, September 15.

Contreras Arias, A.
1942. Mapa de las provincias climatologicas de la República Méxicana. Dir. Meteoro, Hidro. Inst. Geog. México, xxvii + 54 pp.

Cope, E. D.
1861. Contributions to the ophidiology of Lower California, Mexico, and Central America. Proc. Acad. Nat. Sci. Philadelphia, 13: 292-306, December 28.

1887. Catalogue of batrachians and reptiles of Central America and Mexico. Bull. U. S. Natl. Mus., 32:1-98.

Davis, W. B.
1954. Three new anoles from Mexico. Herpetologica, 10:1-6, April 20.

Davis, W. B., and Dixon, J. R.
1957. Notes on Mexican snakes (Ophidia). Southwest. Nat., 2:19-27, January.

Davis, W. B., and Smith, H. M.
1953. Lizards and turtles of the Mexican state of Morelos. Herpetologica, 9:100-108, July 22.

DIXON, J. R.
1957. Geographic variation and distribution of the genus *Tomodactylus* in Mexico. Texas Jour. Sci., 9:379-409, December.

1960. Two new geckos, genus *Phyllodactylus* (Reptilia: Sauria), from Michoacán, Mexico. Southwest. Nat., 5:37-42, April 15.

DOWLING, H. G.
1960. A taxonomic study of the ratsnakes, genus *Elaphe* Fitzinger. VII. The *triaspis* section, Zoologica, 45:53-80, August 15.

DUELLMAN, W. E.
1954a. The salamander *Plethodon richmondi* in southwestern Ohio. Copeia, 1950 (1):40-45, February 19.

1954b. The amphibians and reptiles of Jorullo Volcano, Michoacan, Mexico. Occ. Pap. Mus. Zool. Univ. Michigan, 560:1-24, October 22.

1955. A new whiptail lizard, genus *Cnemidorphorus*, from Mexico. Occ. Pap. Mus. Zool. Univ. Michigan, 574:1-7, December 23.

1956a. The frogs of the hylid genus *Phrynohyas* Fitzinger, 1843. Misc. Publ. Mus. Zool. Univ. Michigan, 96:1-47, February 21.

1956b. A new snake of the genus *Leptotyphlops* from Michoacán, México. Copeia, 1956 (2):93-94, May 29.

1957a. Sexual dimorphism in the hylid frog *Agalychnis dacnicolor* Cope, and the status of *Agalychnis alcorni* Taylor. Herpetologica, 13:29-30, March 30.

1957b. Notes on snakes from the Mexican state of Sinaloa. Herpetologica, 13:237-240, October 31.

1958a. A monographic study of the colubrid snake genus *Leptodeira*. Bull. Amer. Mus. Nat. Hist., 114:1-152, February 24.

1958b. Comments on the type locality and geographic distribution of *Urosaurus gadowi*. Copeia, 1958 (1):48-49, February 21.

1958c. A preliminary analysis of the herpetofauna of Colima, Mexico. Occ. Pap. Mus. Zool. Univ. Michigan, 589:1-22, March 21.

1959. Two new snakes, genus *Geophis*, from Michoacan, Mexico. Occ. Pap. Mus. Zool. Univ. Michigan, 605:1-9, May 29.

1960a. A new subspecies of lizard, Cnemidophorus sacki, from Michoacán, México. Univ. Kansas Publ. Mus. Nat. Hist., 10:587-598, May 2.

1960b. A taxonomic study of the Middle American snake Pituophis deppei, Univ. Kansas Publ. Mus. Nat. Hist., 10: 599-610, May 2.

1960c. Variation, distribution, and ecology of the Mexican teiid lizard *Cnemidophorus calidipes*. Copeia, 1960(2):97-101, June 29.

1960d. A distributional study of the amphibians of the Isthmus of Tehuantepec, México. Univ. Kansas Publ. Mus. Nat. Hist., 13:19-72, August 16.

DUELLMAN, W. E., and DIXON, J. R.
1959. A new frog of the genus *Tomodactylus* from Michoacán, Mexico. Texas Jour. Sci., 11:78-82, March.

DUELLMAN, W. E., and DUELLMAN, A. S.
1959. Notes on the variation, distribution, and ecology of the iguanid lizard *Enyaliosaurus clarki*. Occ. Pap. Mus. Zool. Univ. Michigan, 598:1-10, February 16.

DUELLMAN, W. E., and WELLMAN, J.
1960. A systematic study of the lizards of the *deppei* group (Genus *Cnemidophorus*) in Mexico and Guatemala. Misc. Publ. Mus. Zool. Univ. Michigan, 111:1-80, February 10.

Dugès, A.
1884. Dos reptiles de Mexico. La Naturaleza, 6:359-362.

1891. *Eumeces altamirani* A. Dug. La Naturaleza, ser. 2, 1:485-486.

1896. Reptiles y batracios de los E. U. Mexicanos. La Naturaleza, ser. 2, 2:479-485.

Duméril, A. M., and Bocourt, F.
1870-1909. Mission scientifique au Mexique et dans l'Amerique Centrale, Recherches zoologiques. Études sur les reptiles. Paris, xiv + 1012 pp.

Fischer, J. G.
1882. Herpetologische Bemerkengen vorzugsweise über Stücke der Sammlung des Naturhistorischen Museum in Bremen. Abhand. Naturwiss. Ver. Bremen, 7:225-238.

1883. Beschreibungen neuer Reptilien. Akad. Gymnas. Hamburg, 1883: 1-16.

Fitch, H. S., and Milstead, W. W.
1961. An older name for *Thamnophis cyrtopsis* (Kennicott). Copeia, no. 1:112, March 17, 1961.

Funkhouser, A.
1957. A review of the Neotropical tree-frogs of the genus *Phyllomedusa*. Occ. Pap. Nat. Hist. Mus. Stanford Univ., 5:1-90, April 1.

Gadow, H.
1905. Distribution of Mexican amphibians and reptiles. Proc. Zool. Soc. London, 1905:191-244, October 7.

1930. Jorullo. Cambridge Univ. Press, xviii + 100 pp.

Gloyd, H. K.
1948. Description of a neglected subspecies of rattlesnake from Mexico. Nat. Hist. Misc., 17:1-4, April 23.

Goin, C. J.
1950. Color pattern inheritance in some frogs of the genus *Eleutherodactylus*. Bull. Chicago Acad. Sci., 9:1-15, March 3.

1954. Remarks on evolution of color pattern in the *gossei* group of the frog genus *Eleutherodactylus*. Ann. Carnegie Mus., 33:185-195, June 4.

Goldman, E. A.
1951. Biological investigations in Mexico. Smithsonian Misc. Coll., 115, xii + 476 pp., July 31.

Guzmán-Rivas, P.
1957. Rainfall analysis for some stations in southwest Mexico. *In* Brand, Coastal study of southwest Mexico, Part I. Univ. Texas, Austin, xii + 140 pp., June 15.

Horowitz, S. B.
1955. An arrangement of the subspecies of the horned toad, *Phrynosoma orbiculare* (Iguanidae). Amer. Midl. Nat., 54:209-218, July.

Klauber, L. M.
1945. The geckos of the genus Coleonyx with descriptions of new subspecies. Trans. San Diego Soc. Nat. Hist., 10:133-216, March 9.

1952. Taxonomic studies of the rattlesnakes of Mainland Mexico. Bull. Zool. Soc. San Diego, 26:1-143, August 8.

LANGEBARTEL, D. A.
1959. A new lizard (*Sceloporus*) from the Sierra Madre Occidental of Mexico. Herpetologica, 15:25-27, February 25.

MALDONALDO-KOERDELL, M.
1948. Los colecciones de anfibios del Museo Alfredo Dugès en la Universidad de Guanajuato, I—Urodelos. Mem. Revist. Acad. Nac. Cien., 56:185-226.

MARTIN, P. S.
1958. A biogeography of reptiles and amphibians in the Gómez Farías Region, Tamaulipas, Mexico. Misc. Publ. Mus. Zool. Univ. Michigan, 101:1-102, April 15.

MASLIN, T. P.
1957. *Hyla microeximia* sp. n., Hylidae, Amphibia, from Jalisco, Mexico. Herpetologica, 13:81-86, July 10.

MILSTEAD, W. W.
1953. Geographic variation in the garter snake, *Thamnophis cyrtopsis*. Texas Jour. Sci., 5:348-379, September.

MOSIMANN, J. E.
1956. Variation and relative growth in the plastral scutes of the turtle *Kinosternon integrum* LeConte. Misc. Publ. Mus. Zool. Univ. Michigan, 97:1-43, November 7.

MOSIMANN, J. E., and RABB, G. B.
1953. A new subspecies of the turtle *Geoemyda rubida* (Cope) from western Mexico. Occ. Pap. Mus. Zool. Univ. Michigan, 548:1-7, November 9.

OLIVER, J. A.
1937. Notes on a collection of amphibians and reptiles from the state of Colima, Mexico. Occ. Pap. Mus. Zool. Univ. Michigan, 360:1-28, November 20.

ORTON, G.
1943. The tadpole of *Rhinophrynus dorsalis*. Occ. Pap. Mus. Zool. Univ. Michigan, 472:1-8, May 18.

PETERS, J. A.
1954. The amphibians and reptiles of the coast and coastal sierra of Michoacán, Mexico. Occ. Pap. Mus. Zool. Univ. Michigan, 554:1-37, June 23.

1955. Notes on the frog genus *Diaglena* Cope. Nat. Hist. Misc., 143:1-8, March 28.

1957. The eggs (turtle) and I. Biologist, 39:21-4.

RABB, G. B.
1958. On certain Mexican salamanders of the plethodontid genus *Chiropterotriton*. Occ. Pap. Mus. Zool. Univ. Michigan, 587:1-37, June 6.

RABB, G. B., and MOSIMANN, J. E.
1955. The tadpole of *Hyla robertsorum* with comments on the affinities of the species. Occ. Pap. Mus. Zool. Univ. Michigan, 563:1-9, March 29.

REEVE, W. L.
1952. Taxonomy and distribution of the horned lizards genus *Phrynosoma*. Univ. Kansas Sci. Bull., 34 (pt. 2):817-960, February 15.

SCHMIDT, K. P., and SHANNON, F. A.
1947. Notes on amphibians and reptiles of Michoacán, Mexico. Fieldiana, zool., 31:63-85, February 20.

SHANNON, F. A., and HUMPHREY, F. L.
1957. A new species of *Phrynohyas* from Nayarit. Herpetologica, 13: 15-18, March 30.

1958. A discussion of the polytypic species, *Hypopachus oxyrrhinus*, with a description of a new subspecies. Herpetologica, 14:85-95, July 23.

SMITH, H. M.
1938. The lizards of the *torquatus* group of the genus *Sceloporus* Wiegmann, 1828. Univ. Kansas Sci. Bull., 24:539-693, February 16.

1939. The Mexican and Central American lizards of the genus *Sceloporus*. Zool. ser., Field Mus. Nat. Hist., 26:1-397, July 27.

1941a. A review of the subspecies of the indigo snake (*Drymarchon corais*). Jour. Washington Acad. Sci., 31:466-481, November 11.

1941b. Notes on the snake genus *Trimorphodon*. Proc. U. S. Natl. Mus., 91:149-168, November 10.

1942a. Mexican Herpetological Miscellany. Proc. U. S. Natl. Mus., 92: 349-395, November 5.

1942b. The synonymy of the garter snakes (*Thamnophis*), with notes on Mexican and Central American species. Zoologica, 27:97-123, October 23.

1942c. Remarks on the Mexican king snakes of the triangulum group. Proc. Rochester Acad. Sci., 8:196-207, September 10.

1942d. Descriptions of new species and subspecies of Mexican snakes of the genus *Rhadinaea*. Proc. Biol. Soc. Washington, 55:185-192, December 31.

1943. Summary of the collections of snakes and crocodilians made in Mexico under the Walter Rathbone Bacon Traveling Scholarship. Proc. U. S. Natl. Mus., 93:393-504, October 29.

1951. The identity of the ophidian name *Coluber eques* Reuss. Copeia, 1951 (2):138-140, June 8.

SMITH, H. M., and LAUFE, L. E.
1945. Notes on a herpetological collection from Oaxaca. Herpetologica, 3:1-13, November 21.

SMITH, H. M., and TAYLOR, E. H.
1945. An annotated checklist and key to the snakes of Mexico. Bull. U. S. Natl. Mus., 187:iv + 239 pp., October 5.

1948. An annotated checklist and key to the Amphibia of Mexico. Bull. U. S. Natl. Mus., 194: iv + 118 pp., June 17.

1950a. Type localities of Mexican reptiles and amphibians. Univ. Kansas Sci. Bull., 33, pt. 2:313-380, March 20.

1950b. An annotated checklist and key to the reptiles of Mexico exclusive of the snakes. Bull. U. S. Natl. Mus., 199:v + 253, October 26.

SMITH, P. W., and DARLING, D. M.
1952. Results of a herpetological collection from eastern central Mexico. Herpetologica, 8:81-86, November 1.

STICKEL, W. H.
1943. The Mexican snakes of the genera *Sonora* and *Chionactis*, with notes on the status of other colubrid genera. Proc. Biol. Soc. Washington, 56:109-128, October 19.

STORM, M.
1939. Hoofways into hot country. Bland Bros., Mexico City, 521 pp.

STUART, L. C.
1943. Comments on the herpetofauna of the Sierra de los Cuchumatanes of Guatemala. Occ. Pap. Mus. Zool. Univ. Michigan, 471:1-28, May 17.

Tamayo, J. L.
1949. Geografía General de Mexico. I—Geografía Fisica. Mexico City, viii + 628 pp.

TANNER, W. W.
1944. A taxonomic study of the genus *Hypsiglena*. Great Basin Nat., 5:25-92, December 29.

TAYLOR, E. H.
1936a. New species of amphibia from Mexico. Trans. Kansas Acad. Sci., 39:349-363.

1936b. The rediscovery of the lizard *Eumeces altamirani* (Dugès) with notes on two other Mexican species of the genus. Proc. Biol. Soc. Washington, 49:55-58, May 1.

1936c. A taxonomic study of the cosmopolitan scincoid lizards of the genus *Eumeces*. Univ. Kansas Sci. Bull., 23:1-643, August 15.

1939a. Concerning Mexican salamanders. Univ. Kansas Sci. Bull., 25: 259-313, July 10.

1939b. Frogs of the *Hyla eximia* group in Mexico, with descriptions of two new species. Univ. Kansas Sci. Bull., 25:421-445, July 10.

1940a. A new bromeliad frog from northwestern Michoacan. Copeia, 1940 (1):18-20, March 30.

1940b. Mexican snakes of the genus *Typhlops*. Univ. Kansas Sci. Bull., 26:441-444, November 27.

1940c. Some Mexican serpents. Univ. Kansas Sci. Bull., 26:445-487, November 27.

1940d. Herpetological Miscellany. Univ. Kansas Sci. Bull., 26:489-571, November 27.

1941a. Some Mexican frogs. Proc. Biol. Soc. Washington, 54:87-94, July 31.

1941b. Herpetological Miscellany, No. II. Univ. Kansas Sci. Bull., 27:105-138, December 30.

1942a. New tailless Amphibia from Mexico. Univ. Kansas Sci. Bull., 28: 67-89, May 15.

1942b. Tadpoles of Mexican Anura. Univ. Kansas Sci. Bull., 28:37-55, May 15.

1942c. The frog genus *Diaglena* with a description of a new species. Univ. Kansas Sci. Bull., 28:57-65, May 15.

1943a. Herpetological novelties from Mexico. Univ. Kansas Sci. Bull., 29:343-361, October 15.

1943b. A new *Hylella* from Mexico. Proc. Biol. Soc. Washington, 56:49-52, June 16.

1952. A new hylid frog of the genus *Agalychnis* from southwestern Mexico. Copeia, 1952 (1):31-32, June 2.

1956. A review of the lizards of Costa Rica. Univ. Kansas Sci. Bull., 38 (pt. 1):3-322, December 20.

TAYLOR, E. H., and SMITH, H. M.
1942a. Concerning the snake genus *Pseudoficimia* Bocourt. Univ. Kansas Sci. Bull., 28:241-249, November 12.

1942b. The snake genera *Conopsis* and *Toluca*. Univ. Kansas Sci. Bull., 28:325-363, November 12.

1945. Summary of the collections of amphibians made in Mexico under the Walter Rathbone Bacon Traveling Scholarship. Proc. U. S. Natl. Mus., 95:521-613, June 30.

TIHEN, J. A.
1949. A review of the lizard genus *Barisia*. Univ. Kansas Sci. Bull., 33:217-256, April 20.

VIVÓ, J.
1953. Geografía de México. Mexico City, ed. 3, 338 pp.

WEBB, R. G.
1958. The status of the Mexican lizards of the genus *Mabuya*. Univ. Kansas Sci. Bull., 38:1303-1313, March 2.

WELLMAN, J.
1959. Notes on the variation in and distribution of the Mexican colubrid snake *Coniophanes lateritius*. Herpetologica, 15:127-128, September 10.

WOODBURY, A. M., and WOODBURY, D. M.
1944. Notes on Mexican snakes from Oaxaca. Jour. Washington Acad. Sci., 34:360-373, November 15.

ZWEIFEL, R. G.
1957. A new frog of the genus *Rana* from Michoacán, Mexico. Copeia, 1957 (2):78-83, July 15.

1959a. Variation in and distribution of lizards of western Mexico related to *Cnemidophorus sacki*. Bull. Amer. Mus. Nat. Hist., 117:57-116, April 27.

1959b. Additions to the herpetofauna of Nayarit, Mexico. Amer. Mus. Novitates, 1953:1-13, June 26.

1959c. Snakes of the genus *Imantodes* in western Mexico. Amer. Mus. Novitates, 1961:1-18, September 16.

1960. Results of the Puritan-American Museum of Natural History Expedition to western Mexico. 9. Herpetology of the Tres Marías Islands. Bull. Amer. Mus. Nat. Hist., 119:77-128, February 29.

1961. Relationship of two whiptail lizards (genus *Cnemidophorus*) in western Mexico. Copeia, no. 1:98-103, March 17.

Transmitted April 21, 1961.

(Continued from inside of front cover)

Vol. 8. Nos. 1-10 and index. Pp. 1-675, 1954-1956.

Vol. 9. 1. Speciation of the wandering shrew. By James S. Findley. Pp. 1-68, 18 figures in text. December 10, 1955.

2. Additional records and extensions of ranges of mammals from Utah. By Stephen D. Durrant, M. Raymond Lee, and Richard M. Hansen. Pp. 69-80. December 10, 1955.

3. A new long-eared myotis (Myotis evotis) from northeastern Mexico. By Rollin H. Baker and Howard J. Stains. Pp. 81-84. December 10, 1955.

4. Subspeciation in the meadow mouse, Microtus pennsylvanicus, in Wyoming. By Sydney Anderson. Pp. 85-104, 2 figures in text. May 10, 1956.

5. The condylarth genus Ellipsodon. By Robert W. Wilson. Pp. 105-116, 6 figures in text. May 19, 1956.

6. Additional remains of the multituberculate genus Eucosmodon. By Robert W. Wilson. Pp. 117-123, 10 figures in text. May 19, 1956.

7. Mammals of Coahuila, Mexico. By Rollin H. Baker. Pp. 125-335, 75 figures in text. June 15, 1956.

8. Comments on the taxonomic status of Apodemus peninsulae, with description of a new subspecies from North China. By J. Knox Jones, Jr. Pp. 337-346, 1 figure in text, 1 table. August 15, 1956.

9. Extensions of known ranges of Mexican bats. By Sydney Anderson. Pp. 347-351. August 15, 1956.

10. A new bat (Genus Leptonycteris) from Coahuila. By Howard J. Stains. Pp. 353-356. January 21, 1957.

11. A new species of pocket gopher (Genus Pappogeomys) from Jalisco, Mexico. By Robert J. Russell. Pp. 357-361. January 21, 1957.

12. Geographic variation in the pocket gopher, Thomomys bottae, in Colorado. By Phillip M. Youngman. Pp. 363-387, 7 figures in text. February 21, 1958.

13. New bog lemming (genus Synaptomys) from Nebraska. By J. Knox Jones, Jr. Pp. 385-388. May 12, 1958.

14. Pleistocene bats from San Josecito Cave, Nuevo León, México. By J. Knox Jones, Jr. Pp. 389-396. December 19, 1958.

15. New Subspecies of the rodent Baiomys from Central America. By Robert L. Packard. Pp. 397-404. December 19, 1958.

16. Mammals of the Grand Mesa, Colorado. By Sydney Anderson. Pp. 405-414, 1 figure in text. May 20, 1959.

17. Distribution, variation, and relationships of the montane vole, Microtus montanus. By Emil K. Urban. Pp. 415-511. 12 figures in text, 2 tables. August 1, 1959.

18. Conspecificity of two pocket mice, Perognathus goldmani and P. artus. By E. Raymond Hall and Marilyn Bailey Ogilvie. Pp. 513-518, 1 map. January 14, 1960.

19. Records of harvest mice, Reithrodontomys, from Central America, with description of a new subspecies from Nicaragua. By Sydney Anderson and J. Knox Jones, Jr. Pp. 519-529. January 14, 1960.

20. Small carnivores from San Josecito Cave (Pleistocene), Nuevo León, México. By E. Raymond Hall. Pp. 531-538, 1 figure in text. January 14, 1960.

21. Pleistocene pocket gophers from San Josecito Cave, Nuevo León, México. By Robert J. Russell. Pp. 539-548, 1 figure in text. January 14, 1960.

22. Review of the insectivores of Korea. By J. Knox Jones, Jr., and David H. Johnson. Pp. 549-578. February 23, 1960.

23. Speciation and evolution of the pygmy mice, genus Baiomys. By Robert L. Packard. Pp. 579-670, 4 plates, 12 figures in text. June 16, 1960.

Index Pp. 671-690.

Vol. 10. 1. Studies of birds killed in nocturnal migration. By Harrison B. Tordoff and Robert M. Mengel. Pp. 1-44, 6 figures in text, 2 tables. September 12, 1956.

2. Comparative breeding behavior of Ammospiza caudacuta and A. maritima. By Glen E. Woolfenden. Pp. 45-75, 6 plates, 1 figure. December 20, 1956.

3. The forest habitat of the University of Kansas Natural History Reservation. By Henry S. Fitch and Ronald R. McGregor. Pp. 77-127, 2 plates, 7 figures in text, 4 tables. December 31, 1956.

4. Aspects of reproduction and development in the prairie vole (Microtus ochrogaster). By Henry S. Fitch. Pp. 129-161, 8 figures in text, 4 tables. December 19, 1957.

5. Birds found on the Arctic slope of northern Alaska. By James W. Bee. Pp. 163-211, pls. 9-10, 1 figure in text. March 12, 1958.

6. The wood rats of Colorado: distribution and ecology. By Robert B. Finley, Jr. Pp. 213-552, 34 plates, 8 figures in text, 35 tables. November 7, 1958.

7. Home ranges and movements of the eastern cottontail in Kansas. By Donald W. Janes. Pp. 553-572, 4 plates, 3 figures in text. May 4, 1959.

(Continued on outside of back cover)

(Continued from inside of back cover)

8. Natural history of the salamander, Aneides hardyi. By Richard F. Johnston and Schad Gerhard. Pp. 573-585. October 8, 1959.

9. A new subspecies of lizard, Cnemidophorus sacki, from Michoacán, México. By William E. Duellman. Pp. 587-598, 2 figures in text. May 2, 1960.

10. A taxonomic study of the Middle American Snake, Pituophis deppei. By William E. Duellman. Pp. 599-612, 1 plate, 1 figure in text. May 2, 1960.

Index Pp. 611-626.

Vol. 11. Nos. 1-10 and index. Pp. 1-703, 1958-1960.

Vol. 12. 1. Functional morphology of three bats: Eumops, Myotis, Macrotus. By Terry A. Vaughan. Pp. 1-153, 4 plates, 24 figures in text, July 8, 1959.

2. The ancestry of modern Amphibia: a review of the evidence. By Theodore H. Eaton, Jr. Pp. 155-180, 10 figures in text. July 10, 1959.

3. The baculum in microtine rodents. By Sydney Anderson. Pp. 181-216, 49 figures in text. February 19, 1960.

4. A new order of fishlike Amphibia from the Pennsylvanian of Kansas. By Theodore H. Eaton, Jr., and Peggy Lou Stewart. Pp. 217-240, 12 figures in text. May 2, 1960.

More numbers will appear in volume 12.

Vol. 13. 1. Five natural hybrid combinations in minnows (Cyprinidae). By Frank B. Cross and W. L. Minckley. Pp. 1-18. June 1, 1960.

2. A distributional study of the amphibians of the isthmus of Tehuantepec, México. By William E. Duellman. Pp. 19-72, pls. 1-8, 3 figs. August 16, 1960.

3. A new subspecies of the slider turtle (Pseudemys scripta) from Coahuila, México. By John M. Legler. Pp. 73-84, pls. 9-12, 3 figures in text. August 16, 1960.

4. Autecology of the Copperhead. By Henry S. Fitch. Pp. 85-288, pls. 13-20, 26 figures in text. November 30, 1960.

5. Occurrence of the Garter Snake, Thamnophis sirtalis, in the Great Plains and Rocky Mountains. By Henry S. Fitch and T. Paul Maslin. Pp. 289-308, 4 figures in text. February 10, 1961.

6. Fishes of the Wakarusa River in Kansas. By James E. Deacon and Artie L. Metcalf. Pp. 309-322, 1 figure in text. February 10, 1961.

7. Geographic variation in the North American Cyprinid Fish, Hybopsis gracilis. By Leonard J. Olund and Frank B. Cross. Pp. 323-348, pls. 21-24, 2 figures in text. February 10, 1961.

8. Descriptions of two species of frogs, Genus Ptychohyla—studies of American hylid frogs, V. By William E. Duellman. Pp. 349-357, pl. 25, 2 figures in text. April 27, 1961.

9. Fish populations, following a drought, in the Neosho and Marais des Cygnes rivers of Kansas. By James Everett Deacon. Pp. 359-427, pls. 26-30, 3 figs. in text. August 11, 1961.

More numbers will appear in volume 13.

Vol. 14. 1. Neotropical bats from western México. By Sydney Anderson. Pp. 1-8. October 24, 1960.

2. Geographic variation in the harvest mouse Reithrodontomys megalotis on the central Great Plains and in adjacent regions. By J. Knox Jones, Jr. and B. Mursaloglu. Pp. 9-27, 1 figure in text. July 24, 1961.

3. Mammals of Mesa Verde National Park, Colorado. By Sydney Anderson. Pp. 29-67, pls. 1-2, 3 figures in text. July 24, 1961.

More numbers will appear in volume 14.

Vol. 15. 1. The amphibians and reptiles of Michoacán, México. By William E. Duellman. Pp. 1-148, pls. 1-6, 11 figs. December 20, 1961.

University of Kansas Publications
Museum of Natural History

Volume 15, No. 2, pp. 149-173
January 31, 1962

MUS. COMP. ZOOL.
LIBRARY
FEB 21 1962
HARVARD

Some Reptiles and Amphibians from Korea

BY

ROBERT G. WEBB, J. KNOX JONES, JR.,
AND GEORGE W. BYERS

University of Kansas
Lawrence
1962

University of Kansas Publications, Museum of Natural History
Editors: E. Raymond Hall, Chairman, Henry S. Fitch,
Theodore H. Eaton, Jr.

Volume 15, No. 2, pp. 149-173
Published January 31, 1962

University of Kansas
Lawrence, Kansas

PRINTED BY
JEAN M. NEIBARGER, STATE PRINTER
TOPEKA, KANSAS
1962

28-8517

MUS. COMP. ZOOL
LIBRARY
SEP 3 1962
HARVARD
UNIVERSITY

Some Reptiles and Amphibians from Korea

BY

ROBERT G. WEBB, J. KNOX JONES, JR., AND GEORGE W. BYERS

In 1954, two of us (Jones and Byers) collected reptiles and amphibians in Korea incidental to field studies relating to hemorrhagic fever. The 382 specimens thus obtained were deposited either in the Museum of Natural History of The University of Kansas (KU), or in the Museum of Zoology of the University of Michigan (UMMZ), and are the basis for the present report. Continuous American military operations of one sort or another in Korea since 1945 have afforded opportunities for interested persons to obtain there collections of amphibians and reptiles, the study of which has resulted in several recent publications (Babb, 1955; Dixon, 1956; Hahn, 1959 and 1960; Shannon, 1956 and 1957; Stewart, 1953 and 1954; Tanner, 1953; Walley, 1958*a* and 1958*b*). This paper, which contains comments on the natural history and taxonomy of 22 species, all previously reported from Korea, supplements earlier studies, especially Shannon's (1956) annotated list of the herpetofauna of the country.

Shannon (*loc. cit.*) recorded 36 kinds of reptiles and amphibians from Korea. Subsequently, *Bufo stejnegeri* (previously omitted) was added by Shannon (1957), *Takydromus takydromoides oldi* was described by Walley (1958*a*), and *Takydromus kwangakuensis* was relegated to synonymy under *T. amurensis* by Walley (1958*b*). Presently, then, 37 kinds are on record from the Korean Peninsula.

In the accounts beyond, Jones and Byers are mostly responsible for the remarks on natural history, whereas Webb is mostly responsible for the taxonomic comments. The synonymies include (1) the original description, which is followed by (2) the first use of the name-combination here employed if it differs from the name as originally proposed, and (3) any synonyms having type localities in Korea. All measurements are in millimeters and all dates refer to the year 1954 unless otherwise indicated. A gazetteer of localities mentioned in the text and a list of literature cited follow the accounts of species.

We are grateful to the officers, enlisted men and civilians associated in 1954 with the Field Unit of the Commission on Hemor-

rhagic Fever, Armed Forces Epidemiological Board, who aided our efforts in Korea; we are especially mindful of the contributions of Dr. Albert A. Barber, Dr. Marshall Hertig, Mr. Louis J. Lipovsky and Dr. Warren D. Thomas. We are grateful also to Mr. Yoshinori Imaizumi, National Science Museum of Japan, for his translations of several papers in Japanese, and to Dr. Edward H. Taylor for making certain pertinent references available to us.

Hynobius leechii Boulenger

Hynobius Leechii Boulenger, Ann. Mag. Nat. Hist., ser. 5, 19:67, January, 1887 (type locality, Gensan [= Wonsan], Korea).

Hynobius leechii quelpaertensis Mori, Jour. Chosen Nat. Hist. Soc., 6:47 (Japanese) and 53 (English), March 25, 1928 (type locality, Quelpart Island [= Cheju Do], Korea).

Specimens examined (3).—1 mi. SW Inje, 1 (KU); 4 mi. NNE Sogwi-ri, Cheju Do, 2 (KU).

Description (KU 38774 from 1 mi. SW Inje).—Total length, 86 (head 13, body 40, tail 33); costal grooves (including axillary and inguinal), 13; two costal grooves between adpressed toes; length of inner branch of series of vomerine teeth less than distance between outer border of naris and peak of opposite series (tooth-rows V-shaped, approximately as long as broad); dorsal surface yellowish brown or buff (yellowish in life), having numerous blackish marks; venter yellowish cream, having an indistinct grayish mottling.

Remarks.—The salamander described above was found in a fox-hole with another desiccated individual (not saved) on a military compound on April 24. The only other occurrence of *H. leechii* on the mainland to come to our attention was the report of several larvae that were seen in a small pool on a hillside near Chip'o-ri in the summer of 1953.

Each of the two specimens from Cheju Do (KU 38775-76) differs from KU 38774 in having (1) the length of inner branch of the vomerine series slightly greater than the distance between outer border of naris and peak of opposite series (tooth-rows V-shaped, longer than broad), (2) a dorsal and ventral keel on the tail, (3) one costal groove (rather than two costal grooves) between adpressed toes, and (4) in being darker both dorsally and ventrally. The area of buff on the dorsal surface of each specimen is reduced by a fine, blackish mottling and stippling, and the venter of each is grayish. Respective total lengths of KU 38775 and 38776 are 84 (head 12, body 36, tail 36) and 89 (12, 35, 42), and the number of costal grooves 13 and 14. Although the two specimens are of approximately the same size, the tail of KU 38776 is noticeably the longer; the tail of KU 38775 is thicker and deeper than that of KU 38776.

The two specimens from 4 mi. NNE Sogwi-ri were taken on September 9 in damp substrate under volcanic rocks along a little-used road; although many rocks were overturned, only these two individuals were found. A South Korean soldier informed us that salamanders were fairly common on Cheju Do.

Mori (1928*a*:16) first mentioned in Japanese text the alleged distinctiveness of the salamander occurring on Cheju Do. Later, Mori (1928*b*:47 in Japanese, and 1928*c*:53 in English) provided valid descriptions of the subspecies, *Hynobius leechii quelpaertensis*. Okada (1934:17) questioned the validity of *H. l. quelpaertensis* and Sato (1943) regarded the salamanders of Cheju Do as inseparable from the Korean *H. leechii*. The English description of *quelpaertensis* is briefer than the preceding one in Japanese and lacks comparisons with related forms. KU 38775-76 seemingly differ appreciably from the description of *quelpaertensis* only in having the series of vomerine teeth narrowly V-shaped and longer than broad. We tentatively follow Sato in regarding *quelpaertensis* as a synonym of *leechii*.

Bombina orientalis (Boulenger)

Bombinator orientalis Boulenger, Ann. Mag. Nat. Hist., ser. 6, 5:143, pl. IX, fig. 2, February, 1890 (type locality restricted to Chefoo, China, by Pope, Bull. Amer. Mus. Nat. Hist., 61:435, August 29, 1931).

Bombina orientalis, Stejneger, Bull. U. S. Nat. Mus., 58:51, figs. 30-43, pl. VII (reproduction from Boulenger, *supra*), July 22, 1907.

Specimens examined (87).—2 mi. N Chip'o-ri, 8 (KU), 5 (UMMZ); 1 mi. SW Inje, 1 (KU); 15 mi. NE Mosulp'o, Cheju Do, 6 (KU); Sangdaehwa, 2 (KU); Taehoesan-ni, 1 (KU); 1 mi. W Tangjonggok, 32 (KU), 17 (UMMZ); Tangnim-ni, 2 (KU); 3 mi. SW Yanggu, 1 (KU); 2 mi. N Yongdae-ri, 8 (KU), 4 (UMMZ).

Remarks.—Most of our specimens were taken from breeding congresses after heavy rains in rice fields and other shallow temporary waters. Thirteen individuals from Chip'o-ri were collected from foxholes around the edge of a military compound (two pairs in amplexus; no egg masses seen), and represent a small sample of frogs that were everywhere following a heavy rain on the night of May 13-14. On April 23, 32 *Bombina orientalis* and three *Rana temporaria dybowskii* were trapped in the water-filled bottom of an unused grease pit near Tangjonggok. Many tadpoles and two kinds of egg masses (small clusters and beadlike strings) were present; the small clusters of *Bombina* were commonest. On June 13 at the same locality, thousands of these toads were observed (hundreds in axillary amplexus) in foxholes, temporary rain pools, and backwashes along the Puk-ch'on [river]. On June 12 near

Yongdae-ri many individuals were seen (several pairs in amplexus), along Route 24 paralleling the Puk-ch'on, in rain pools and in ditches and backwashes from the river; almost all available water contained small (approximately 10 x 10 mm.) egg masses. Numbers of eggs per mass, selected at random, were 5, 2, 2, 5, 2, 8, 8, 2 and 5. Some that were saved subsequently hatched on June 15-17.

The call is a quiet low trill or series of staccato whistles rising slightly at the beginning; a short peeplike note also was heard. The specimens from Cheju Do, which are generally smaller than those collected on the mainland in spring, were taken on September 6 in a small stream that had large volcanic rocks in many places and that was flanked by thick brush and small trees. The earliest and latest dates on which *B. orientalis* was collected were April 21 and September 6, respectively.

In the breeding season, males are distinguished from females by the large blackish (probably brownish earlier in season) areas on the anteroventral surface of the antebrachium, the metacarpal tubercle, and the inner surface of the first finger (sometimes also the second and third). Also, males have conspicuous black-tipped tubercles on the back (usually absent in females) that extend onto the limbs (usually smooth in females, at least laterally). Field observations by one of us (Byers) suggested that the dorsal pattern of males had greater contrast than that of females and that the venter was brighter reddish. Eight females from Tangjonggok averaged 47.9 (43-51) in snout-vent length, whereas 24 males from there averaged 50.0 (46-55), indicating little, if any, size difference between the sexes.

Okada (1931:29) recorded variation in color of live Korean individuals (green or brown dorsally and pale yellow or red ventrally) and variation in extent of black markings on the belly (*op. cit.*:fig. 12). The specimens from Cheju Do (28, 32, 32, 32, 37 and 46 in snout-vent length) have less black ventrally than specimens from the mainland.

Bufo bufo gargarizans Cantor

Bufo gargarizans Cantor, Ann. Mag. Nat. Hist., ser. 1, 9:483, August, 1842 (type locality, island of Chusan, China).

Bufo bufo gargarizans, Stejneger, Bull. U. S. Nat. Mus., 58:59, July 22, 1907.

Specimens examined (10).—Central National Forest, near Pup'yong-ni, 1 (KU); 5 mi. NW Choksong, near Imjin River, 1 (KU); 5 mi. E Seoul, 1 (KU); 6 mi. E Seoul, 4 (KU), 2 (UMMZ); 1 mi. S Yami-ri, 1 (KU).

Description (nine females).—Dorsal surface brownish, having indistinct pale areas, some of which tend to form longitudinal stripes that extend pos-

teriorly from parotoid glands; blackish mark, usually on lateral part of parotoid, having short spurs directed posteriorly and ventrally; edge of upper jaw and warts on dorsal surface becoming blackish with increasing size; small, conspicuous group of warts near angle of jaw below parotoid; middorsal warts tending, at level of posterior edge of parotoids, to form a V that has its apex between the parotoids; ventral surface pale yellowish, sometimes having well-defined blackish marks; granular underparts of large specimens having small blackish tubercles.

Male (KU 40118 from 5 mi. E Seoul).—Snout-vent length, 65; no vocal sacs or slits; dorsal and inner surfaces of first and second fingers, and inner surface of third finger black; canthus rostralis indistinct (a well-defined ridge on right side); nostrils closer to tip of snout than to eye, their distance from each other slightly less than interorbital width; interorbital width (6.2) greater than width of eyelid (4.7); tympanum distinct, circular, its diameter (3.0) less than length of eye (6.5), and approximately twice distance (1.6) of tympanum from eye; no cranial crests; parotoid gland elongate, approximately twice as long as broad (12.5 x 5.0), narrowly separated from posterior edge of eyelid; head elongate (width at posterior edge of tympanum, 23.6); length from posterior edge of tympanum to tip of upper jaw, 18.9; first finger slightly longer than second, fourth finger about two-thirds as long as third; most subarticular tubercles divided; outer palmar tubercle larger than inner; heels not touching when folded legs placed at right angles to longitudinal axis of body; tibiotarsal articulation just reaching eye when leg laid forward; tarsometatarsal articulation not reaching beyond snout; foot large (tibiotarsal articulation to tip of fourth toe approximately 46.0); fourth toe approximately half webbed, other toes more than half webbed; edges of webs somewhat crenulate; some subarticular tubercles divided; length of inner metatarsal tubercle (4.5) more than half length of first toe (7.0); inner metatarsal tubercle larger than outer, both darkened; tarsal fold extending from inner metatarsal tubercle for approximately two-thirds length of tarsus; tips of toes (not fingers) darkened; dorsal surface of back and proximal part of hind legs coarsely granular, of rounded, pavement-type tubercles lacking sharp tips; small group of warts near angle of jaw below parotoids; dorsal pattern contrasting and irregular (especially on limbs), of dark brown and pale gray; conspicuous black mark (interrupted) on lateral surface of parotoid having two, well-defined spurs that project posteroventrally; undersurface granular, lacking markings except for two indistinctly-margined dark spots on chest, and black spot on left leg.

Remarks.—This nocturnal, introduced species (Okada, 1931:47) is presumably widespread in Korea and seemingly prefers lowland habitats. Individuals were taken in sparse vegetation on a sand flat near the Han River, at the edge of a rice field in a light rain, along a road at night, and in millet fields adjacent to the Han River, which was flooding at that time (July 9).

As is obvious from the foregoing descriptions, the male (KU 40118), which was obtained on March 19, differs considerably from the nine females; neither does it agree with Stejneger's (1907:66)

or Okada's (*op. cit.*:45-46, fig. 18) description of males of *Bufo bufo asiaticus* [= *gargarizans*] from Wonsan and Seoul. Upon cursory examination, KU 40118 is notable for having a contrasting dorsal pattern and elongate, ranidlike proportions. Some of the characteristics resemble those of *Bufo raddei* Strauch as given by Stejneger (*op. cit.*:70-72, figs. 53-57), Okada (1935:9, figs. 2 and 32-34, pls. II-III), and Liu (1950:203-205, fig. 43).

Stejneger (*op. cit.*:59-68) recognized *B. b. gargarizans* as occurring in southern China, and *Bufo bufo asiaticus* as the subspecies occurring in northern China. Subsequently, *asiaticus* was relegated to synonymy under the earlier-named *gargarizans*—see discussions by Pope and Boring (1940:33) and Liu (*op. cit.*:220).

Kaloula borealis (Barbour)

Cacopoides borealis Barbour, Bull. Mus. Comp. Zool., 51(12):231, April, 1908 (type locality, Antung, Manchuria).

Kaloula borealis, Noble, Amer. Mus. Novit., 165:6, April 16, 1925.

Specimens examined (8).—5 mi. ESE Seoul, 1 (KU); 6 mi. E Seoul, 3 (UMMZ); 7 mi. ESE Seoul, 4 (KU).

Remarks.—On April 5, one male and three females were uncovered by a bulldozer from between one and two feet below the surface of the ground in an old Korean burial mound; one individual was completely surrounded by compact soil. All quickly became active when placed in water. Two of the females (43 and 44 in snout-vent length) contained masses of immature eggs. A male obtained on June 4 was found during a rain; the three UMMZ specimens were obtained on July 8 on banks above the Han River. Breeding of this species seems to coincide with the rainy season in late spring and early summer when males were noted calling around flooded ditches and swales in deep grass. The local Korean name of the species, which sounds something like "maeng-kongi," is said to come from the call, which is best described as a monotonous, snoring sound that rarely is heard in two parts as suggested by the name.

Hyla arborea japonica Günther

[*Hyla arborea*] Var. *japonica* Günther, Catalogue of the Batrachia Salientia in the . . . British Museum, p. 109, 1858 (type locality, Japan).

Hyla arborea var. *savignyi* Boulenger, Ann. Mag. Nat. Hist., ser. 5, 19:67, January, 1887 (type locality, Gensan [= Wonsan], Korea).

Hyla stepheni Boulenger, Proc. Zool. Soc. London, p. 579, pl. 51, fig. 1 (for 1887), April, 1888 (type locality, Port Hamilton, a small island between Korea and Japan).

Specimens examined (44).—Central National Forest, near Pup'yong-ni, 2 (KU); 3 mi. NW Chip'o-ri, 1 (KU); 1 mi. N Mosulp'o, Cheju Do, 1 (KU);

1 mi. NW Oho-ri, 13 (KU), 3 (UMMZ); Sangbonch'on-ni, 2 (UMMZ); 5 mi. ESE Seoul, 8 (KU); 6 mi. E Seoul, 10 (KU), 3 (UMMZ); 7 mi. NNE Sogwi-ri, Cheju Do, 1 (UMMZ).

Remarks.—Hylids from 5 mi. ESE Seoul were collected from a cement-walled pit at the Seoul City Water Works; a specimen of *Elaphe rufodorsata* taken in the pit had eaten one hylid. Two individuals were taken in the morning of May 29 on leaf litter in a wooded valley in the Central National Forest where a number were calling in a light rain, but the species was rarely found in woods. Two frogs were found along a rocky stream at Sangbonch'on-ni. Most individuals were taken while calling, on grasses and reeds or on the ground, along the edges of rice fields. Sixteen hylids collected 1 mi. NW Oho-ri were calling in shallow water of a rice field on a hillside, but none was heard in a large lake nearby or in adjacent fields. On May 15, 4 mi. ESE Ch'orwon, approximately one hundred tadpoles, thought to be of this species, congregated near a drain (into a lower field) of an unused rice field; the tadpoles were well-developed, some having hind legs. The earliest and latest dates of collection represented in our material are May 8 and October 29. The call is best described as a raspy "waak," "week," or "wiick" in the middle register.

The listing of "Hylae arboreae var japonicae descript pars *Schleg. in Fauna Japon.* p. 112 . . ." by Günther (1858:81) in synonymy under the account of *Polypedates schlegelii,* implies that Schlegel was the first author to use the name-combination *Hyla arborea japonica.* Boulenger (1882:86, 381) went so far as to credit Schlegel as the author of the name *japonica.* The reason for this action is not known because Schlegel (*in* von Siebold, 1838:112) referred to this hylid only under the name "Hyla arborea."

Rana rugosa Schlegel

Rana rugosa Schlegel, Reptilia [Saurii et Batrachii], *in* von Siebold, Fauna Japonica, p. 110, pl. 3, figs. 3-4, 1838 (type locality designated as Japan, probably near Nagasaki, by Stejneger, Bull. U. S. Nat. Mus., 58:123, July 22, 1907).

Specimens examined (26).—Central National Forest, near Pup'yong-ni, 13 (KU), 1 (UMMZ); 2 mi. S Ch'orwon, 4 (KU); 2 mi. E Hoengsong, 3 (KU); 1 mi. NW Oho-ri, 1 (KU); 5 mi. ESE Seoul, 1 (KU); 6 mi. E Seoul, 3 (UMMZ).

Remarks.—*Rana rugosa* was associated with *Rana nigromaculata* and *Rana amurensis coreana* at all localities where the species was taken save at 2 mi. E Hoengsong, where *R. a. coreana* was not observed. Three specimens of *R. rugosa* were collected among

grasses and reeds in water along the edge of Ch'orwon Reservoir, 2 mi. S Ch'orwon, where they were difficult to find in the thick vegetation even though their low, soft calls were heard; the specimen from 1 mi. NW Oho-ri was found in a rice field. Otherwise, habitats recorded indicate a preference for small, fast-flowing streams, especially in wooded valleys. On one occasion, individuals were found trapped in cement-walled pits about old ruins on a wooded hillside in the Central National Forest. The earliest and latest dates of capture among our specimens are May 15 and November 6. In addition to the localities listed above, the species was observed 4 mi. W Ch'ungju.

R. rugosa may have an extensive breeding season as suggested by the variation in size of frogs collected or observed in 1954. Of nine frogs obtained on May 29, five ranged in snout-vent length from 26 to 28, and four from 42 to 54. Three specimens collected on October 9 measured 39, 41, and 55, and two obtained on November 6 measured 25 and 37.

Rana nigromaculata Hallowell

Rana nigromaculata Hallowell, Proc. Acad. Nat. Sci. Philadelphia, [12]:500 (for 1860), 1861 (type locality, Simoda, Japan).

Specimens examined (47).—Central National Forest, near Pup'yong-ni, 6 (KU); 2 mi. S Ch'orwon, 5 (KU); 4 mi. W Ch'ungju, 2 (KU); 7 mi. W Ch'ungju, 1 (KU); 2 mi. E Hoengsong, 1 (KU); 8 mi. SW Kunsan, 1 (KU); 1 mi. NW Oho-ri, 5 (KU); 5 mi. ENE Pusan, 2 (KU); 5 mi. ESE Seoul, 9 (KU); 6 mi. E Seoul, 3 (KU), 10 (UMMZ); 6 mi. NNE Sogwi-ri, Cheju Do, 2 (KU).

Description.—Back brownish or grayish (greenish in life), having few, indistinct or well-defined, dark blotches, or extensive blackish areas (representing fusion of markings); pale, middorsal stripe (pale green, buff or yellowish in life) from snout to anus, sometimes as wide as interorbital width, but indistinct or lacking when pattern on back absent; blackish bar often present behind tympanum; posterior surface of thigh mottled; underparts pale yellow to whitish, sometimes having a few dusky marks on throat; longitudinal ridges between dorsolateral folds indistinct in some small frogs; largest female and male having respective snout-vent lengths of 100 and 70.

Remarks.—*Rana nigromaculata* is the most abundant ranid in central Korea and, in a general way, the ecological equivalent of *Rana pipiens* in temperate North America. The species is associated with most aquatic habitats, from rocky streams to rice fields and large impoundments. In the vicinity of Seoul the din of large breeding congresses was heard more or less continuously from mid-April to mid-May. Large numbers of juveniles (approximately one inch long) were noticed first on July 8 and were present

thereafter for about three weeks, being commonest in standing water after heavy rains or during prolonged showers. These data and the different sizes of individuals collected at the same time suggest either variable growth or, more probably, an extensive breeding season. Our earliest and latest dates of collection are April 16 and October 7. The Korean name for "frog," most often applied to *R. nigromaculata,* sounds something like "keg-oh-ree." The call is a prolonged, raspy, staccato croak, sometimes with a rising inflection at the end.

In addition to the localities listed above, the species was observed 5 mi. W Kwangju and 3 mi. S Osan.

Despite a high degree of individual variation, *Rana nigromaculata* seemingly varies geographically as well; some subspecies probably should be recognized, but the species as a whole has never been thoroughly studied systematically. The division of *R. nigromaculata* into three subspecies by Schmidt (1927:563-567) was considered untenable by Fang and Chang (1931:95-98), and it has been regarded by most recent authors as a variable, monotypic species.

The named subspecies *R. n. chosenica* (Okada, 1931:89, with type locality at Seoul, and geographically restricted to Korea) was considered a subspecies of *Rana plancyi* by Shannon (1956:36). The most trenchant characters of *planyci* seem to be the wide dorsolateral folds, the uniform greenish dorsum, the presence of dermal pustules on the back between the dorsolateral folds, and the lack of a mottled pattern on the posterior surface of the thigh. Among our specimens of *R. nigromaculata,* the width of the dorsolateral folds is variable, a uniform greenish dorsum is found only in large males, dermal pustules are mixed with ridges in only one male (KU 38733), and all have a spotted or mottled pattern on the posterior surface of the thigh. All of our specimens having an indistinct pattern on the back, or lacking a pattern, are males and resemble the photographs of males published by Moriya (1954: pl. I, fig. 5) and Liu (1936: pl. IV, figs. 1-2); juveniles of both sexes and large females have contrasting patterns.

None of our frogs seems, therefore, clearly referable to the species *plancyi,* although some characters are suggestive of *plancyi.* Moriya (*op. cit.*:19), who studied variation of *R. nigromaculata* in Japan, noted that one of the most distinct populations there (*R. n. brevipoda*) resembled *Rana plancyi.* Ting (1939) discovered that *nigromaculata* and *plancyi* were cross-fertile and raised hybrid

larvae through metamorphosis. Pope and Boring (1940) suggested hybridization between the two species in eastern China, and the above mentioned facts suggest to us the possibility of hybridization in other regions.

Rana amurensis coreana Okada

Rana temporaria coreana Okada, Annot. Zool. Japon., 11:140 (footnote), July 25, 1927, *nomen nudum.*

Rana temporaria coreana Okada, Jour. Chosen Nat. Hist. Soc., 6:19, pl. 1, fig. 7, 1928 (type locality, Keijo [= Seoul], Korea).

Rana amurensis coreana, Shannon, Herpetologica, 12:38, March 6, 1956.

Specimens examined (9).—Central National Forest, near Pup'yong-ni, 1 (KU); 2 mi. S Ch'orwon, 1 (KU); 4 mi. W Ch'ungju, 1 (KU); 1 mi. N Oho-ri, 1 (KU); 5 mi. ESE Seoul, 3 (KU); Yongp'yong, 2 (KU).

Remarks.—One individual of *R. a. coreana* (KU 38698) and one of *Rana temporaria dybowskii* (KU 38715) were collected on May 29 along a stream in the Central National Forest in association with *R. rugosa* and *R. nigromaculata.* Specimens of *coreana* from the vicinity of Seoul were found in rice fields. The earliest date of collection was April 13 at Yongp'yong. Our largest specimen of *coreana* measured 47 in snout-vent length.

Because *R. a. coreana* and *Rana temporaria dybowskii* are sympatric in central Korea and closely resemble one another, the two species were not distinguished in the field and the following observations may pertain to either (or both) species. Wood frogs were observed 2 mi. E Songdong-ni on July 12 in paddies (rice fields) along with individuals of *Hyla arborea, Rana rugosa,* and *Rana nigromaculata.* At Chip'o-ri on April 6, individuals (probably *R. t. dybowskii*) were seen in a seepage pool from an abandoned rice field; *R. nigromaculata* also was seen there. Six or seven egg masses (some having small tadpoles) were observed in the shallow water, but it was not certain to which species the eggs belonged. Completely metamorphosed young (probably *R. a. coreana*) were first seen 1 mi. N Oho-ri on June 9. At Taehoesan-ni on November 12, several sluggish frogs were seen in a small pool that was covered by a thin layer of ice.

On September 26 in the Central National Forest, many wood frogs of various sizes were observed. *R. amurensis* and *R. temporaria* probably have extended breeding seasons that correspond to those of *R. rugosa* and *R. nigromaculata.* Judging from our observations, *amurensis* prefers the proximity of water, whereas *temporaria* may occur some distance from permanent water.

In our specimens, *R. amurensis coreana* differs from *R. temporaria*

dybowskii in having (1) smaller maximal size, (2) more slender body, (3) shorter legs, (4) incompletely webbed toes, (5) no mottling or barring on lips, (6) no contrasting barred pattern on hind legs, (7) dark brown stripes (usually) between dorsolateral folds, (8) a dark brown, linear mark below canthus, and (9) an immaculate ventral surface. Two additional distinguishing characters, which we found difficult to evaluate, are the nearly straight, dorsolateral folds, and lack of vocal sacs or ostia in males of *R. a. coreana* (Shannon, 1956:38). Some of the differences between the two species were illustrated by Okada, 1931:107, fig. 48, *R. temporaria temporaria* [= *R. t. dybowskii*] and 123, fig. 54, *R. temporaria coreana* [= *R. amurensis coreana*].

Rana temporaria dybowskii Günther

Rana Dybowskii Günther, Ann. Mag. Nat. Hist., ser. 4, 17:387, May, 1876 (type locality, Abrek Bay, near Vladivostok, Siberia).

Rana temporaria dybowski, Shannon, Herpetologica, 12:38, March 6, 1956.

Specimens examined (20).—Central National Forest, near Pup'yong-ni, 7 (KU); Chip'o-ri, 2 (KU); 1 mi. SW Inje, 6 (KU); 8 mi. SW Kangnung, 1 (KU); Taegwang-ni, 1 (KU); 1 mi. SW Tangjonggok, 3 (KU).

Remarks.—On October 9 in the Central National Forest, five individuals were found in a concrete-walled pit in old ruins on a wooded hillside; no specimens of *Rana amurensis coreana* were taken there. *R. t. dybowskii* was most often taken on high, moist slopes, and seemed to be especially common in forests. The specimen from 8 mi. SW Kangnung was obtained in a wooded area along a mountain stream. The earliest date of collection of a specimen of *dybowskii* was March 7 at Taegwang-ni. See also the remarks under the preceding account of *Rana amurensis coreana.*

The largest male among our specimens measured 65 in snout-vent length and the largest female, 79. Five gravid females had snout-vent lengths of 64, 68, 69, 69 and 70.

Trionyx sinensis Wiegmann

Trionyx (Aspidonectes) sinensis Wiegmann, Nova Acta Acad. Leopold.-Carol., 17:189, 1835 (type locality, near Macao, China).

Specimen examined.—Han River, 5 mi. ESE Seoul, 1 (KU).

Remarks.—Our only specimen was purchased from a man who had captured it by hand in the Han River; it was the only turtle seen during our stay in Korea. Koreans eat turtles, and the elaborate (and relatively permanent) fish-traps that they construct across streams and small rivers probably reduce the size of populations of *T. sinensis* and other species.

Eremias argus Peters

Eremias argus Peters, Monatsber. preuss. Akad. Wiss., Berlin, p. 61, fig. 3 (for 1869), 1870 (type locality, Chefoo, China).

Specimens examined (23).—Chip'o-ri, 1 (KU); 5 mi. E Seoul, 3 (KU), 3 (UMMZ); 5 mi. ESE Seoul, 4 (KU); 6 mi. E Seoul, 10 (UMMZ); 7 mi. ESE Seoul, 2 (KU).

Remarks.—Individuals of *E. argus* were most often seen on dry hillsides having a relatively sparse cover of vegetation. The first lizard of this species was taken on April 2. In 1954 the last part of March and early part of April were generally warm, with temperatures above 70° F. on several occasions; probably some *E. argus* were active in late March. KU 38773 (snout-vent length, 51) laid three eggs between June 4 and 14; KU 38768 (snout-vent length, 58) obtained on May 8 was gravid, containing four eggs. Testes of lizards in the breeding season measure approximately 4.0 x 2.5 (KU 38772, obtained on June 16).

The snout-vent length of our largest female is 61, that of the largest male, 57. The snout-vent length of 11 specimens averaged 77 (67-96) per cent of length of tail.

Tachydromus amurensis Peters

Tachydromus amurensis Peters, Sitzungsber. Gesell. naturf. Freunde Berlin, p. 71, 1881 (type locality, Kossakewitcha, Amurland).

Specimens examined (3).—Central National Forest, near Pup'yong-ni, 1 (KU), 1 (UMMZ); Majon-ni, 1 (KU).

Remarks.—One of our specimens was found among grasses along a small stream in the Central National Forest. The other two were obtained by other persons and we lack knowledge of conditions of their capture.

A juvenile (KU 39416, snout-vent length, 25) that was obtained on September 9 is tentatively referred to this species. There seem to be three femoral pores on the left leg but the number is indistinct on the right. The specimen is dark and lacks a pattern. Its condition precludes counts of ventral scales (not keeled), but scalation is otherwise the same as a male (KU 40120, snout-vent length approximately 47, length of tail, 124). The third specimen, a male (UMMZ 113442, snout-vent length, 51, length of tail, 115), agrees with KU 40120, except in having 32 instead of 29 dorsal scales at midbody, 4-4 instead of 3-3 femoral pores, and in lacking a pale stripe from eye through ear to shoulder.

Tachydromus wolteri Fischer

Tachydromus Wolteri Fischer, Jahrb. Wiss. Anst. Hamburg, 2:82 (for 1884), 1885 (type locality, Chemulp'o, Korea).

Specimens examined (2).—Yongp'yong, 2 (KU).

Remarks.—On April 14, two females (57 and 45 in snout-vent length, the tail of the latter measuring 103) were easily captured by hand on a burned-over rice field.

Lygosoma reevesii (Gray)

Tiliqua Reevesii Gray, Ann. [Mag.] Nat. Hist., ser. 1, 2:292, December, 1838 (type locality, China).

[*Lygosoma* (*Liolepisma*) *laterale*] var. *reevesi*, Boettger, Katalog der Batrachier-Sammlung . . ., p. 104, 1893.

Specimens examined (6).—Central National Forest, near Pup'yong-ni, 3 (KU); 4 mi. NNE Sogwi-ri, Cheju Do, 1 (KU); 7 mi. NNE Sogwi-ri, Cheju Do, 1 (UMMZ); 16 mi. NE Mosulp'o, Cheju Do, 1 (UMMZ).

Remarks.—On October 23 an individual was captured while sunning on a stump on a wooded hillside in the Central National Forest; two others at this locality were collected on damp ground-cover on the same hillside. A juvenile from Cheju Do was found among moss-covered rocks in a stream bed; the other specimens from Cheju Do were found among moss-covered rocks on the western slope of Halla San.

Each ovary of a female obtained on October 23 contained five enlarged follicles, about 1 mm. in diameter. The left testis of a male obtained on August 10 seemed enlarged, indicating possible sexual activity, and measured approximately 6 x 2 mm. The snout-vent length of our largest male is 41, that of our largest female, 48. The prefrontals are in contact in all of our specimens save one (UMMZ 113446).

There is disagreement among herpetologists concerning the generic name of the small lygosome skink in the United States and its ecological equivalent in China and Korea. We tentatively use *Lygosoma* (Conant, 1951:207-208), although Mittleman (1950) pointed out reasons for using *Scincella*. Shannon (1956:41) discussed the debated issue whether or not the lygosome skinks of the New and Old worlds are conspecific.

Rhabdophis tigrina lateralis (Berthold)

Tropidonotus lateralis Berthold, Nachrichten Gesell. Wiss. Göttingen, p. 180, 1859 (type locality, China).

Specimens examined (26).—Central National Forest, near Pup'yong-ni, 1 (KU); 2 mi. N Chip'o-ri, 2 (KU); 3 mi. NW Chip'o-ri, 4 (KU); 4 mi. N Ch'onan, 1 (KU); 3 mi. S Kumhwa, 1 (KU); 1 mi. SW Naegong-ni, 1 (KU); 4 mi. E Seoul, 1 (KU); 5 mi. E Seoul, 2 (UMMZ); 5 mi. ESE Seoul, 4 (KU); 6 mi. E Seoul, 1 (KU), 4 (UMMZ); 7 mi. ESE Seoul, 1 (KU); 6 mi. NNE Sogwi-ri, Cheju Do, 2 (KU); 5 mi. NE Taejon, 1 (KU).

Remarks.—This common, vagrant species was found on brushy hillsides, near buildings on hills above rice fields, in tall grasses near streams, in rice fields, and along drainage and irrigation ditches. The earliest and latest dates of collection were April 5 and November 7. On the first date mentioned an individual was found in hibernation with five *Elaphe rufodorsata* and one *Agkistrodon halys* in an earthen Korean burial mound. The specimen was uncovered by a bulldozer at a depth of about one foot below the surface. We were told that 18 snakes of this species were found in the same place (7 mi. ESE Seoul) the previous winter.

The stomach of each of four individuals contained one *Rana nigromaculata.* The stomach of another individual contained a *R. nigromaculata* and remains of a carabid beetle, whereas another contained three small, partially-digested frogs that appeared to be *Hyla arborea.* P. M. Youngman reported to us that he found a snake of this species that was attempting to swallow a toad, *Bufo bufo gargarizans.* One of the small individuals from Cheju Do was being eaten by a *Zamenis spinalis* when found. One specimen was parasitized by three nematodes, *Kalicephalus natricis* (see Olsen, 1957:208).

Two females of this oviparous species (lengths of body, 680 and 700) collected on May 14 contained nine eggs (18 mm. long), and 13 eggs (15 mm.) respectively; a third (length of body, 610) obtained on June 26 contained 10 eggs that were approximately 18 mm. long. A female (UMMZ 113458, length of body, 710), which was captured on July 10 and kept alive in captivity, laid 11 eggs on August 12 between 9 and 10 in the morning. The weight of nine of these eggs averaged 3.32 (3.0-3.6) grams; the last two eggs deposited were small and weighed only 1.3 and 1.4 grams. The eggs were incubated unsuccessfully. One that was opened on September 14 and another opened on September 26 contained young easily recognized as of this species. In captivity the parent

snake underwent ecdysis on about July 20 and again on August 26.

Our largest female and largest male have respective total lengths of 1013 (840 + 173) and 740 (575 + 165). Our smallest specimens, captured on September 9, measured 215 and 230 mm. in length of body, and probably represent young of the year. The snake found in hibernation on April 5 measured 275 in length of body. The ventrals of 11 males averaged 161.3 (158-171) and those of 14 females, 165.1 (160-170); subcaudals of eight males averaged 69.6 (66-74) and those of 14 females, 61.5 (52-73).

Males seem to have small scales in the anal region that are more strongly keeled than scales elsewhere on the body (the scales catch on finger tips when rubbed in a posteroanterior direction), but males lack small tubercles on the upper and lateral parts of the head as mentioned by Maslin (1950:433). The comments of the same author (*op. cit.*:434) concerning integumental poison glands in the nuchal region of this species are of interest in view of several reports that we received of swollen extremities resulting from handling snakes of this species.

In using the generic names *Rhabdophis* and *Amphiesma* for species formerly placed in the genus *Natrix*, we follow Malnate (1960), who divided *Natrix* (*auct.*) into five distinct genera.

Amphiesma vibakari ruthveni (Van Denburgh)

Natrix vibakari ruthveni Van Denburgh, Proc. California Acad. Sci., ser. 4, 13(2):3, July 26, 1923 (type locality, Pusan, Korea).

Specimens examined (5).—Central National Forest, near Pup'yong-ni, 1 (KU); 4 mi. SW Ch'ongyang-ni, 1 (KU); 10 mi. NE Mosulp'o, Cheju Do, 1 (UMMZ); 6-7 mi. NNE Sogwi-ri, Cheju Do, 1 (KU), 1 (UMMZ).

Remarks.—The specimen from the Central National Forest was captured on August 18 near a stream on a damp ground-cover of leaves. The specimens from Cheju Do were taken in early September, one in a grassy area, and the other two on earthen banks of road-cuts on the slopes of Halla San. The stomach of one individual from Cheju Do contained an earthworm. Our largest specimen, a male having 154 ventrals and 68 subcaudals, measured 508 (380 + 128).

The subcaudal counts of 68 (KU 38861) and 69 (UMMZ 113461) on two males from Cheju Do are higher than the maximal count known for the subspecies *ruthveni* in Korea, and resemble those of *Amphiesma vibakari vibakari* of the Japanese islands. The subcaudals average 61 (55-65) in *ruthveni* and 71 (63-83) in *vibakari*

according to Van Denburgh (1923:3-4). A juvenile from the Central National Forest (KU 38862), lacking the tip of the tail, has 64 subcaudals.

Dinodon rufozonatum (Cantor)

Lycodon rufo-zonatus Cantor, Ann. Mag. Nat. Hist., ser. 1, 9:483, August, 1842 (type locality, island of Chusan, China).

Dinodon rufozonatus, Peters, Sitzungsber. Gesell. naturf. Freunde Berlin, p. 89, 1881.

Specimens examined (4).—Central National Forest, near Pup'yong-ni, 3 (KU); Yongsan (Seoul), 1 (UMMZ).

Remarks.—The three specimens from the Central National Forest were taken in the period August 12-26. Two were caught in live-traps set for small mammals in deep forest among granite outcrops. The specimen from Yongsan was obtained on October 27 in a partly wooded area. Ventrals and subcaudals of our four specimens (all males) numbered, respectively, 198, 200, 198, 205, and 74, 75, 75, —. Total length of the largest specimen was 960 (790 + 170).

We follow Chang (1932:54) and most subsequent authors in regarding *D. rufozonatum* as a monotypic species.

Zamenis spinalis (Peters)

Masticophis spinalis Peters, Monatsber. preuss. Akad. Wiss., Berlin, p. 91 (for 1866), 1867 (type locality, unknown—"Mexico" erroneously listed).

Zamenis spinalis, Günther, Ann. Mag. Nat. Hist., ser. 4, 9:22, January, 1872.

Specimens examined (2).—5 mi. ESE Seoul, 1 (KU); 6 mi. NNE Sogwi-ri, Cheju Do, 1 (KU).

Remarks.—The specimen from Cheju Do was captured on September 9 in tall grass near a small stream and was eating a small *Rhabdophis tigrina.* The female from near Seoul was obtained from a Korean on June 10, and was gravid (six eggs, each approximately 35 mm. in length). The length of body measured approximately 550 and the length of incomplete tail 168 in one specimen (KU 38777, female from 5 mi. ESE Seoul), 540 and 183 in the other (KU 38778, female from Cheju Do). Respective ventral and subcaudal counts of the two females are 204, 194, and 74 +, 86.

There is some disagreement in the literature as to the proper generic name of this snake. Differences in dentition between Old World species (referable to *Zamenis*) and the American species (referable to *Coluber*) are discussed by Bogert and Oliver (1945: 365). The species *spinalis* has been referred to *Coluber* by several authors (see Pope, 1935:226).

Elaphe dione (Pallas)

Coluber dione Pallas, Reise durch verschiedene Provinzen des Russischen Reichs, 2:717, 1773 (type locality, "Salt steppes toward the Caspian Sea" according to Stejneger, Bull. U. S. Nat. Mus., 58:315, July 22, 1907).

Elaphis dione, Duméril and Bibron, Erpétologie générale . . ., 7:248, 1854.

Specimens examined (10).—Choksong, 1 (KU); 4 mi. N Ch'onan, 1 (KU); Seoul, 1 (KU); 5 mi. E Seoul, 1 (KU), 2 (UMMZ); 5 mi. ESE Seoul, 1 (KU); 6 mi. E Seoul, 1 (UMMZ); Taegwang-ni, 1 (KU); 2 mi. WSW Tongjonggok, 1 (KU).

Remarks.—This species seemingly occurs in upland habitats. Specimens were taken on rocky hillsides, on sparsely wooded hillsides, and in cultivated fields. November 21 was the latest date of capture of an active individual (UMMZ 113451), the head of which was seen many times prior to capture protruding from a hole beneath the concrete floor of a building. A female (KU 38855), measuring 915 (775 + 140) in total length, and obtained on June 13, contained nine eggs (32 mm. long). One juvenile had eaten a half-grown house mouse, *Mus musculus;* the stomach of a male contained three mice, one a striped field mouse, *Apodemus agrarius,* the other two probably also of that species but too far digested for certain identification. Eggs probably hatch in late summer. A young of the year (length of body, 340) was captured on September 30; another juvenile (length of body, 285) was obtained in May.

Our largest male (KU 40123) measured 904 (719 + 185) in total length. Ventrals and subcaudals of six females averaged 205.8 (198-211) and 62.2 (55-69), respectively, whereas corresponding counts of four males averaged 196.8 (190-214), and 71.0 (69-74). Each of nine specimens had dorsal scales in 23-25-19 rows except one (UMMZ 113451), which had 23-25-23 rows.

Elaphe rufodorsata (Cantor)

Tropidonotus rufodorsatus Cantor, Ann. Mag. Nat. Hist., ser. 1, 9:483, August, 1842 (type locality, island of Chusan, China).

Elaphe rufodorsata, Stejneger, Bull. U. S. Nat. Mus., 58:310, figs. 269-271, July 22, 1907.

Specimens examined (27).—7 mi. NW Changhowan-ni, 1 (KU); 3 mi. NW Chip'o-ri, 3 (KU); 7 mi. W Ch'ungju, 2 (KU), 1 (UMMZ); 3 mi. S Kumhwa, 2 (KU); 1 mi. NW Oho-ri, 1 (KU); 4 mi. E Seoul, 1 (KU); 5 mi. E Seoul, 2 (KU); 5 mi. ESE Seoul, 2 (KU); 6 mi. E Seoul, 3 (KU), 2 (UMMZ); 7 mi. ESE Seoul, 5 (KU); 4 mi. N Uijongbu, 1 (KU); 5 mi. NE Uijongbu, 1 (UMMZ).

Remarks.—*E. rufodorsata* was commonly observed and collected on barren hillsides, on country roads, in rice fields, and along drain-

age ditches and small streams. One was found sunning outstretched on a road. Two individuals were trapped in cement-walled pits at the Seoul City Water Works. On April 5, five snakes of this species with one *Rhabdophis tigrina* and one *Agkistrodon halys,* all partly caked with earth, were found sunning in a shallow depression on the side of a Korean burial mound, which was presumably a hibernaculum. Aside from one juvenile, four of the *E. rufodorsata* were of approximately the same size, having bodies ranging in length from 385 to 455.

Copulation was observed on April 25 (male, KU 38811, length of body, 400, and female, KU 38812, length of body, 565), and on May 4 (female, KU 38816, length of body, 620). Eggs doubtless hatch at various times in summer. One of five snakes obtained on April 5 (see above) measured 310 (250 + 60) in total length. Another juvenile (KU 38828), obtained on October 18, was 478 (385 + 93) long, and our smallest specimen of this species (KU 38821), captured on June 26, measured 275 (230 + 45).

The stomachs of two snakes each contained a *Rana nigromaculata;* another individual had eaten a *Hyla arborea,* and a fourth specimen had eaten a small fish. One specimen was parasitized by a cestode.

The largest female from our series (KU 38816) measured 740 (620 + 120), and the largest male (KU 38813), 595 (475 + 120). Respective ventral and subcaudal counts of 13 males averaged 170.5 (167-174) and 60.0 (56-63), ventrals of 12 females averaged 178.3 (169-182), and subcaudals of 11 averaged 51.0 (46-56).

Elaphe schrencki anomala (Boulenger)

Coluber anomalus Boulenger, Ann. Mag. Nat. Hist., ser. 8, 17:243, March, 1916 (type locality, Chihfeng, China).

Elaphe schrencki anomala, Pope, The reptiles of China, p. 266, fig. 57, May 11, 1935.

Specimens examined (7).—Central National Forest, near Pup'yong-ni, 2 (KU), 1 (UMMZ); 4½ mi. W Chip'o-ri, 1 (KU); 5 mi. N P'yong-taek, 1 (KU); 5 mi. E Seoul, 1 (KU); 5 mi. ESE Seoul, 1 (KU).

Remarks.—Individuals were observed or taken on dry, scrubby hillsides and in grassy upland areas. One of the three snakes from the Central National Forest was captured on a steep, forested hillside among granite outcroppings; another was obtained there along a stream bank and had eaten three bats, *Murina aurata* (see Jones, 1960:265), and one mouse, *Apodemus* sp. (tail only found). P. M. Youngman reported (personal communication) finding a rat (*Rattus* sp.) in the stomach of one individual. A female (KU 38830, length

of body, 1180) that was obtained on June 2 contained 17 eggs, each approximately 32 mm. long. The ventrals of two females numbered 223 and 229, and the subcaudals of the latter 70. Ventrals and subcaudals of five males were, respectively, 211, 213, 214, 215, 216, and 71, 75, 75, 69, 75.

The coloration and pattern of our seven specimens are of interest in view of the probable intergradation between *E. s. anomala* and *E. s. schrencki* in northern Korea (see comments by Shannon, 1956: 46). The smallest specimen (KU 38831), having a total length of 335 (280 + 55), was obtained 4 mi. N P'yong-taek on September 24. It is nearly uniform pale brown (lacks a dorsal pattern) and additionally is characterized as follows: incomplete pattern on the head; no black postocular band (pale brown with black posterior border); ventrolateral extensions of the head pattern that form longitudinal stripes of white on the third row of scales; a pale whitish stripe on the sixth and seventh scale rows that extends posteriorly to the level of the fortieth ventral and that has a narrow black border (sometimes interrupted); small and indistinct blackish markings and pale stripes on sides (no higher than sixth row of scales); underside of the head whitish; and venter grayish, having blackish margins on the ends of ventrals posteriorly. KU 38831 is unusual and perhaps anomalous in having a pattern that does not conform to the juvenal pattern of either subspecies.

A female (KU 38830), having a total length of 1390 (1180 + 210), from 5 mi. ESE Seoul conforms to descriptions of *anomala* in being uniformly pale brown above and in having indistinct dark smudges on the sides; the ventral surface is whitish having indistinct dark smudges, brown spots at the ends of each ventral, and the posterior edge of each ventral brown. A male (KU 40125), measuring 1090 (890 + 200) in total length, from 5 mi. E Seoul, is pale brown above and lacks markings on the anterior part of the body. Indistinct dark markings occur at midbody, whereas the posterior quarter of the body and tail have well-defined black bands on a buff background. The black bands posteriorly are arranged in pairs; each pair of bands is separated by two and a half to three scales, whereas the bands of each pair are separated by only one and a half scales. The ventral surface has an obscure marbled pattern. Our largest specimen, a male (UMMZ 113454) having a total length of 1488 (1230 + 258), from the Central National Forest, resembles KU 40125, except that pale brown blotches (29 on body, one blackish on neck) and dark lateral spots occur anteriorly on the body.

Another female (KU 38860, body length, 970) from 4½ mi. W Chip'o-ri, our northernmost locality of record, has a fairly distinct pattern dorsally. The 30 dark brown, black-edged blotches that are separated by a buff background are not arranged in pairs (as in KU 40125); the dorsal blotches sometimes alternate with small lateral blotches. The ventral surface is marbled throughout.

Two males from the Central National Forest, having total lengths of 1105 (920 + 185) and 830 (690 + 140), generally resemble one another in having the head and neck dark brown or blackish and the anterior part of body dark brown, but discernibly blotched. The posterior part of the body and tail of each bears well-defined blotches (dark brown or black) with buffy interspaces; the dorsal blotches are sometimes arranged in pairs. The ventral surface of each is marbled throughout. These two males are noteworthy in that the pattern anteriorly is obscure, but the ground color is dark, not pale as in the two specimens from the vicinity of Seoul.

Agkistrodon halys brevicaudus Stejneger

Agkistrodon blomhoffii brevicaudus Stejneger, Bull. U. S. Nat. Mus., 58:463, July 22, 1907 (type locality, Pusan, Korea).

Agkistrodon halys brevicaudus, Okada, A catalogue of vertebrates of Japan, p. 103, 1938.

Specimens examined (12).—Central National Forest, near Pup'yong-ni, 4 (KU); 3 mi. NW Chip'o-ri, 2 (KU); 16 mi. NE Mosulp'o, Cheju Do, 1 (UMMZ); 5 mi. E Seoul, 1 (UMMZ); 6 mi. E Seoul, 2 (KU); 7 mi. ESE Seoul, 1 (KU); 7 mi. NNE Sogwi-ri, Cheju Do, 1 (UMMZ).

Remarks.—Individuals of *Agkistrodon* were collected on brushy or wooded hillsides, along rock walls or in piles of rocks, and in damp, rocky, wooded ravines near streams. Many were docile when captured. One specimen was infested with nematodes, another with cestodes. One specimen had eaten a striped field mouse, *Apodemus agrarius*, and another had eaten a gray hamster, *Cricetulus triton*. One female, obtained on May 22, 6 mi. E Seoul, contained 14 embryos. Another female, obtained on August 25 in the Central National Forest, contained three well-developed embryos.

We have not included descriptive or taxonomic remarks concerning *A. halys* because Dr. Howard K. Gloyd, University of Arizona, who currently is studying the systematics of the genus *Agkistrodon*, has our specimens on loan.

Gazetteer

Listed below are all localities mentioned in the accounts of species; the latitude (north) and longitude (east) are given for each. All place-names can be found in "Gazetteer to maps of Korea," 3 vols., AMS 2, U. S. Army Map Service, September, 1950, and, except for the two marked by an asterisk, can be located on AMS map series L552 (Korea, 1:250,000). The McCune-Reischauer system of romanization of Korean names is used.

Changhowan-ni. 37°07′, 127°38′
Central National Forest. A small mixed forest 15-18 mi. NE Seoul and immediately west of the village of Pup'yong-ni; most of our collecting there was done approximately at 37°45′, 127°10′
Cheju Do (Quelpart Island). A large island in the East China Sea off the southwestern tip of the Korean mainland (see Mosulp'o and Sogwi-ri)
Chip'o-ri. 38°08′, 127°19′
Choksong. 37°58′, 126°57′
Ch'onan. 36°48′, 127°09′
*Ch'ongyang-ni. 38°15′, 127°23′
Ch'orwon. 38°15′, 127°13′
Ch'ungju. 36°58′, 127°57′
Halla San. A central, volcanic mountain on Cheju Do (see above)
Hoengsong. 37°29′, 127°59′
Inje. 38°04′, 128°11′
Kangnung. 37°45′, 128°54′
Kumhwa. 38°17′, 127°28′
Kunsan. 35°59′, 126°43′
Kwangju. 35°09′, 126°55′
Majon-ni. 37°52′, 126°46′
Mosulp'o. 33°13′, 126°15′
Naegong-ni. 37°41′, 127°10′
Oho-ri. 38°20′, 128°32′
Osan. 37°09′, 127°04′
Pup'yong-ni. 37°44′, 127°12′
Pusan. 35°08′, 129°04′
P'yong-taek [= P'yongt'aeng-ni]. 36° 59′, 127°05′
Sangbonch'on-ni. 37°27′, 127°16′
Sangdaehwa. 37°30′, 128°26′
Seoul. 37°32′, 127°00′
Sogwi-ri. 33°15′, 126°34′
Songdong-ni. 38°01′, 127°16′
Taegwang-ni. 38°11′, 127°06′
*Taehoesan-ni. 38°04′, 127°14′
Taejon. 36°20′, 127°26′
Tangjonggok. 38°11′, 128°19′
Tangnim-ni. 37°50′, 127°37′
Uijongbu. 37°44′, 127°03′
Wonsan. 39°09′, 127°27′
Yami-ri. 38°03′, 127°16′
Yanggu. 38°06′, 128°00′
Yongdae-ri. 38°13′, 128°23′
Yongp'yong. 38°01′, 127°13′

Literature Cited

BABB, G. H., JR.
1955. An annotated checklist of the amphibians and reptiles of Korea. Bull. Philadelphia Herp. Soc., 1:17-23.

BOGERT, C. M., AND OLIVER, J. A.
1945. A preliminary analysis of the herpetofauna of Sonora. Bull. Amer. Mus. Nat. Hist., 83:297-426, 8 pls., 13 figs., 2 maps, March 30.

BOULENGER, G. A.
1882. Catalogue of the Batrachia Salientia s. Ecaudata in the collection of the British Museum. Taylor and Francis, London, xvi + 503 pp., 30 pls.

CHANG, M. L. Y.
1932. Notes on a collection of reptiles from Szechuan. Contrib. Biol. Lab., Sci. Soc. China, Zool. Ser., 8:9-95, 28 figs., February.

CONANT, R.
1951. The reptiles of Ohio. Second edition (with revisionary addenda). Amer. Midland Nat., Univ. Notre Dame Press, 284 pp., 27 pls.

DIXON, J. R.
1956. A collection of amphibians and reptiles from west central Korea. Herpetologica, 12:50-56, 1 fig., March 6.

FANG, P. W., AND CHANG, M. L. Y.
1931. Amphibia of Nanking. Contrib. Biol. Lab., Sci. Soc. China, Zool. Ser., 7:65-114, 18 figs., May.

GÜNTHER, A.
1858. Catalogue of the Batrachia Salientia in the collection of the British Museum. Taylor and Francis, London, xvi + 160 pp., 12 pls.

HAHN, D. E.
1959. Observations and collecting notes on *Rana n. nigromaculata* in central Korea. Jour. Ohio Herp. Soc., 2:7-8, September 20.
1960. Collecting notes on central Korean reptiles and amphibians. Jour. Ohio Herp. Soc., 2:16-24, 4 figs., September 20.

JONES, J. K., JR.
1960. The least tube-nosed bat in Korea. Jour. Mamm., 41:265, May 20.

LIU, C.
1936. Secondary sex characters of Chinese frogs and toads. Zool. Ser., Field Mus. Nat. Hist., 22:115-156, 12 pls., October 31.
1950. Amphibians of western China. Fieldiana: Zool. Memoirs, Chicago Nat. Hist. Mus., 2:1-400, 10 pls., 100 figs., June 15.

MALNATE, E. V.
1960. Systematic division and evolution of the colubrid snake genus *Natrix*, with comments on the subfamily Natricinae. Proc. Acad. Nat. Sci. Philadelphia, 112:41-71, 2 figs., 4 maps, September 23.

MASLIN, T. P.
1950. Snakes of the Kiukiang-Lushan area, Kiangsi, China. Proc. California Acad. Sci., ser. 4, 26:419-466, 10 figs., April 28.

MITTLEMAN, M. B.
1950. The generic status of *Scincus lateralis* Say, 1823. Herpetologica, 6:17-20, June 5.

MORI, T.
1928*a*. A presumption of the age in which the separation of Japan and Korea had occurred and the general condition at that age estimated from the distribution of animals in Saishuto and Tsushima. Chosen, pp. 14-25, January, 1928 (in Japanese).
1928*b*. On amphibians and reptiles of Quelpaert Island. Jour. Chosen Nat. Hist. Soc., 6:47-52, March 25 (in Japanese).
1928*c*. On a new Hynobius from Quelpaert Isl. Jour. Chosen Nat. Hist. Soc., 6:53, March 25.

MORIYA, K.
1954. Studies on the five races of the Japanese pond frog, *Rana nigromaculata* Hallowell. I. Differences in the morphological characters. Jour. Sci. Hiroshima Univ. (ser. B, div. 1), 15:1-21, 2 pls., 1 fig., December.

OKADA, Y.
1931. The tailless batrachians of the Japanese Empire. Imp. Agric. Exp. Sta., Tokyo, 215 pp., 29 pls., 97 figs., March 30.
1934. A contribution toward a check list of the urodeles of Japan. Copeia, 1934 (1):16-19, April 24.
1935. Amphibia of Jehol. Rept. First Sci. Exped. Manchoukuo, sect. V, div. II, pt. II, art. 1, pp. 1-24 (in Japanese) and 25-47 (in English), 7 pls., 9 figs., November 30.

OLSEN, L. S.
1957. A new species of *Neoascaris* (Nematode) from a Korean wood mouse. Trans. Amer. Micros. Soc., 76:205-208, 9 figs., April.

POPE, C. H.
1935. The reptiles of China (Natural History of Central Asia, Vol. X). Amer. Mus. Nat. Hist., New York, lii + 604 pp., 27 pls., 78 figs., May 11.

POPE, C. H., AND BORING, A. M.
1940. A survey of Chinese Amphibia. Peking Nat. Hist. Bull., 15:13-86, 1 map, September.

SATO, I.
1943. The tailed batrachians of Japan. Tokyo, 520 pp., illustrated (in Japanese).

SCHLEGEL, H.
1838. Reptilia (*in* von Siebold, Fauna Japonica), pp. 1-144, illustrated.

SCHMIDT, K. P.
1927. Notes on Chinese amphibians. Bull. Amer. Mus. Nat. Hist., 54: 553-575, 2 pls., October 14.

SHANNON, F. A.
1956. The reptiles and amphibians of Korea. Herpetologica, 12:22-49, 1 pl., 1 fig., March 6.
1957. Addition to the herpetofauna of Korea. Herpetologica, 13:52, March 30.

STEJNEGER, L.
1907. Herpetology of Japan and adjacent territory. Bull. U. S. Nat. Mus., 58:xx + 577, 35 pls., 409 figs., July 22.

STEWART, G. D.
1953. Notes on a collection of amphibians from central Korea. Herpetologica, 9:146-148, October 30.
1954. A small collection of reptiles from central Korea. Copeia, 1954 (1):65-67, February 19.

TANNER, V. M.
1953. Pacific Islands herpetology No. VIII, Korea. Great Basin Nat., 13:67-73.

TING, H.
1939. A study of the reciprocal hybrids of two species of frogs, *Rana nigromaculata* and *Rana plancyi*. Peking Nat. Hist. Bull., 13: 181-200, 3 pls., March.

VAN DENBURGH, J.
1923. A new subspecies of watersnake (*Natrix vibakari ruthveni*) from eastern Asia. Proc. California Acad. Sci., ser. 4, 13:3-4, July 26.

WALLEY, H. D.
1958*a*. A new lacertid lizard from Korea. Herpetologica, 14:203-205, 1 fig., December 1.
1958*b*. "The status of *Takydromus kwangakuensis* Doi." Copeia, 1958 (4):338, December 22.

Transmitted June 30, 1961.

MUS. COMP. ZOO
LIBRARY
JUL 12 196
UNIVERSITY

University of Kansas Publications
Museum of Natural History

Volume 15, No. 3, pp. 175-181, 1 fig.
March 7, 1962

A New Species of Frog (Genus Tomodactylus) from Western México

BY

ROBERT G. WEBB

University of Kansas
Lawrence
1962

University of Kansas Publications, Museum of Natural History
Editors: E. Raymond Hall, Chairman, Henry S. Fitch,
Theodore H. Eaton, Jr.

Volume 15, No. 3, pp. 175-181, 1 fig.
Published March 7, 1962

University of Kansas
Lawrence, Kansas

PRINTED BY
JEAN M. NEIBARGER, STATE PRINTER
TOPEKA, KANSAS
1962

29-1923

MUS. COMP. ZOOL
LIBRARY
JUL 12 1962
HARVARD
UNIVERSITY

A New Species of Frog (Genus Tomodactylus) from Western México

BY

ROBERT G. WEBB

Thirteen specimens of frogs collected in the summers of 1960 and 1961 in the Mexican states of Durango and Sinaloa represent a heretofore unnamed species. The specimens have been deposited in the Museum of Natural History of the University of Kansas (KU) and in the Museum of Michigan State University (MSU). The species may be named and described as follows:

Tomodactylus saxatilis new species

Holotype.—KU 63326 (Fig. 1); obtained eight miles west of El Palmito, Sinaloa, approximately 6100 feet, on 23 June 1961; original field number, 2354 of Robert G. Webb.

Paratypes.—A total of 12 specimens: KU 63327-33, same data as holotype, 23-25 June 1961; MSU 4085-88, two miles north of Pueblo Nuevo, Durango, approximately 6000 feet elevation, 24 July 1960; MSU 4089, one half mile west of Revolcaderos, Durango, approximately 6600 feet, 29 July 1961.

Diagnosis.—A species of *Tomodactylus* possessing the following combination of characters: (1) tips of two outer fingers truncate, about twice width of narrowest part of digit; (2) tympanum small, less than one half diameter of eye; (3) ventral surfaces smooth; (4) contrasting marbled pattern on back and top of head, and (5) venter whitish, lacking dark marks.

Description of holotype.—Adult male; snout-vent length, 31.5 (measurements are in millimeters and were taken by means of dial calipers reading to one tenth of a millimeter); width of head, 11.2; length of head, 10.3; horizontal diameter of eye, 3.1, and of tympanum, 1.2; distance from eye to nostril, 3.8; internarial width, 2.9; interorbital width, 4.1; width of eyelid, 2.5; lumbar gland (left side), 7.0 x 2.6; distance from axilla to groin, 15.2; tibial length, 12.7; length of foot, 13.1.

Head slightly wider than body; tip of snout rounded, slightly truncate; canthus rounded; tympanum small, less than one half diameter of eye; tympanum having posterior margin ill-defined, separated from eye by distance about equal to diameter of tympanum; diameter of eye slightly less than distance from eye to nostril; width of eyelid about two thirds interorbital width; paratoid gland indistinct; lumbar glands high, separated from insertion of leg by about one millimeter; back and sides of body having low, scarcely elevated pustules; top of head, limbs and venter smooth; few low, whitish pustules below and behind tympanum, and low on sides of body; posterior surface of thighs and anal region pustulate; one pair of whitish postanal spots; ventral disc attached near insertion of legs, lacking conspicuous transverse fold; skin loose on throat, chest and abdomen.

Digits not webbed; tips of two outer fingers truncate, having terminal transverse grooves, about twice width of narrowest part of digit; digits of first and second fingers slightly expanded; fingers from shortest to longest, 1-2-4-3, first only slightly shorter than second; three palmar tubercles; inner palmar tubercle about one third size of large median tubercle; outer tubercle about one tenth size of large median tubercle; four supernumerary palmar tubercles; tips of toes slightly wider than narrowest part of digits; toes from shortest to longest, 1-2-5-3-4, second only slightly shorter than fifth; inner metatarsal tubercle about four times size of small outer metatarsal tubercle; supernumerary tubercles on foot small; no tarsal fold; heels touching when tibiae adpressed to thighs; tibiotarsal articulation reaching eye when leg adpressed to side of body.

Contrasting marbled pattern on back and top of head; contrasting, mostly barred, pattern on limbs; ventral surfaces whitish, lacking dark marks, but having minute dark peppering; marbling of dorsal surfaces blackish and whitish in preservative.

Vomerine teeth lacking; internal choanae lateral, partly concealed by maxillaries; tongue smooth, elongate, shallowly notched distally, free for about half its length; vocal sac median; internal vocal slits large and near angle of jaw.

Variation.—Twelve males closely resemble the holotype. Two specimens from Pueblo Nuevo are soft and not well preserved. The ranges of variation (means in parentheses) for the 13 males comprising the type series are: snout-vent length, 25.5-31.5 (27.9); width of head, 9.7-11.2 (10.5); diameter of eye, 2.9-3.6 (3.2); horizontal diameter of tympanum, 1.1-1.8 (1.4); length of tibia, 11.1-13.1 (12.1); length of foot, 11.0-13.1 (12.1).

The pale ground color of the marbled pattern in most specimens is least extensive on the back and arms, but most extensive on the legs. The lumbar glands are slightly elevated and conspicuous, and in KU 63328 are extremely protuberant, or (KU 63330) evident on left side but flattened and indistinct on right side. The back is rough having low, scarcely elevated pustules, but becomes less rough anteriorly and most of the top of head is smooth. The three specimens from Pueblo Nuevo, Durango, differ slightly from the other specimens examined in lacking pairs of postanal white spots, and in having smooth backs (slightly pustulate in MSU 4088). The tibiotarsal articulation fails to reach the eye in KU 63330. The small inner palmar tubercle is continuous with the large median tubercle on the right hand of KU 63330, and lacking on both hands of KU 63329 and on the left hand of KU 63328. The tip of the tongue is entire in some specimens and in others has an irregular margin.

Coloration of living specimens.—Marbled pattern on back and top of head of dark brown to blackish on yellowish-gold; pattern slightly less contrasting on limbs than on back, consisting of brown to grayish on pale yellow; side of head and body grayish sometimes having pale yellow to whitish spots; iris blackish having fine reticulation of yellowish to greenish-gold; venter dirty white.

Habitat.—The three records of occurrence for *Tomodactylus saxatilis* are in a mixed boreal-tropical habitat, which is transitional between a pine-oak forest at higher elevations and a tropical decidu-

ous forest at lower elevations. The mixed boreal-tropical habitat is most conspicuous at elevations between approximately 7800 and 5500 feet on southerly exposed slopes of barrancas and arroyos of the dissected plateau of the Sierra Madre Occidental. The mixed boreal-tropical habitat occurs for approximately 30 miles along the paved highway (Mexican Highway 40) between Cd. Durango, Durango, and Mazatlán, Sinaloa. The records of occurrence in those states that are along this highway are separated by 14.5 miles (*via* road).

Fig. 1. *Tomodactylus saxatilis* new species, adult male, KU 63326, holotype (× 2), dorsal view.

The terrain consists of occasional level areas, but is mostly of steep hillsides. Dominant trees are large oaks and pines; a characteristic pine is the sad or drooping-needle pine, locally called "pino triste." The vegetational cover is usually open, including grasses, small oaks and pines, broad-leaved shrubs and herbs, prickly pears, magueys, thorny acacias, bracken fern, and epiphytes in trees. Ferns occur in moist protected places, and orchids are occasional, sometimes in trees.

Outcrops of rock, boulder-strewn areas, and occasional rock slides (talus) also characterize the terrain. *Tomodactylus saxatilis* seems to be restricted to rocky habitats. The individuals collected were detected when they called at night from within crevices of rocks or from exposed perches on rocks and boulders; some calling frogs were out of reach on steep rock walls. The call is a single, loud, high peep.

Comparisons.—Dixon (1957) recognized six species of *Tomodactylus* (*nitidus, dilatus, albolabris, angustidigitorum, fuscus* and *grandis*) in his revision of the genus. Another species (*rufescens*) was subsequently described by Duellman and Dixon (1959). *Tomodactylus saxatilis* differs from all the species named immediately above by the combination of characters given in the diagnosis. *Tomodactylus saxatilis* differs from *nitidus, angustidigitorum* and *grandis* in having the tips of the two outer fingers widened and truncate; *saxatilis* differs from *dilatus, albolabris, fuscus* and *rufescens* in having a smooth venter (not pustulate), a contrasting pale and dark marbled pattern on the back, and a lack of "flash" colors on the femora.

Tomodactylus saxatilis, having lumbar glands, also resembles three species referred to the genus *Syrrhophus. Tomodactylus macrotympanum* was described by Taylor (1940:496, 497) as having a large, moderately distinct lumbar gland; the species was referred to the genus *Syrrhophus* by Dixon (*op. cit.*:384). According to Firschein (1954:55), *Syrrhophus smithi* and *S. petrophilus* have elongate lumbar glands shaped like those in *Tomodactylus. Tomodactylus saxatilus* resembles *macrotympanum, smithi* and *petrophilus* more than it does other species; all four attain large maximal sizes, and have lumbar glands, mostly smooth ventral surfaces, three palmar tubercles (sometimes absent in *saxatilis*), and usually contrasting dorsal patterns (reduced to flecks and spots in all species except *saxatilis*). *Tomodactylus saxatilis* differs from *macrotympanum* in having an extensive marbled dorsal pattern and a small tympanum, and differs from *smithi* and *petrophilus* in having a marbled dorsal pattern and the tips of the outer two fingers widened and truncate. *Tomodactylus saxatilis* differs from all other named species of *Syrrhophus* in having conspicuous lumbar glands and in lacking inguinal glands.

Remarks.—The characteristics delimiting the genera *Tomodactylus* and *Syrrhophus* are not agreed upon by all workers (see discussions by Firschein, 1954:50; Langebartel and Shannon, 1956:164; and Dixon, 1957:383). I have referred *saxatilis* to the genus *Tomodactylus* on the basis of a lumbar gland, which was considered a distinguishing character for the genus by Smith and Taylor (1948:46) and Langebartel and Shannon (1956:165). Lumbar glands are longer than broad, at least one third the distance from axilla to groin, lateral and usually high, and often conspicuous and protuberant. The elevation or flatness of the lumbar glands seems to be due to individual variation; living specimens in the field had conspicuous and protuberant, or non-elevated, indistinct lumbar glands. Lumbar glands are not to be confused with inguinal glands,

which are roundish, often yellowish, sometimes diffuse, lateral but low, often inconspicuous, and usually not protuberant. Inguinal glands occur in the genus *Microbatrachylus* and in some species of *Eleutherodactylus*, and have been described as flat, or low, or small, or indistinct for most species of *Syrrhophus*.

For financial assistance with field work I am grateful to Rollin H. Baker, and those individuals who administer the Michigan State University Development Fund and the Bache Fund of the National Academy of Sciences (Grant No. 463). I am grateful also to J. Keever Greer, Donald F. Switzenberg, and Rudolph A. Scheibner for aid in the field, to Edward H. Taylor, James R. Dixon, and William E. Duellman for profitable discussions, and to Thomas Sweringen for figure 1. The specific name alludes to the habitat (Latin, *saxatilis* = found among rocks).

LITERATURE CITED

Dixon, J. R.
1957. Geographic variation and distribution of the genus Tomodactylus in Mexico. Texas Journ. Sci., 9(4):379-409, 5 figs., 1 map, December.

Duellman, W. E., and Dixon, J. R.
1959. A new frog of the genus *Tomodactylus* from Michoacan, Mexico. Texas Journ. Sci., 11(1):78-82, 1 fig., 1 table, March.

Firschein, I. L.
1954. Definition of some little-understood members of the leptodactylid genus *Syrrhophus*, with a description of a new species. Copeia, 1954, 1:48-58, February 19.

Langebartel, D. A., and Shannon, F. A.
1956. A new frog (*Syrrhophus*) from the Sinaloan lowlands of Mexico. Herpetologica, 12(3):163-165, 2 figs., September 1.

Smith, H. M., and Taylor, E. H.
1948. An annotated checklist and key to the Amphibia of Mexico. Bull. U. S. Nat. Mus., No. 194, pp. iv + 118.

Taylor, E. H.
1940. Herpetological miscellany. Univ. Kansas Sci. Bull., 26(15):489-571, 10 pls., 7 figs., November 15.

29-1923

FEB - 6 1963

University of Kansas Publications
Museum of Natural History

Volume 15, No. 4, pp. 183-204
October 26, 1962

Type Specimens of Amphibians and Reptiles in the Museum of Natural History, The University of Kansas

BY

WILLIAM E. DUELLMAN AND BARBARA BERG

University of Kansas
Lawrence
1962

University of Kansas Publications, Museum of Natural History
Editors: E. Raymond Hall, Chairman, Henry S. Fitch,
Theodore H. Eaton, Jr.

Volume 15, No. 4, pp. 183-204
Published October 26, 1962

University of Kansas
Lawrence, Kansas

PRINTED BY
JEAN M. NEIBARGER, STATE PRINTER
TOPEKA, KANSAS
1962
29-4227

LIBRARY
FEB - 6 1963

Type Specimens of Amphibians and Reptiles in the Museum of Natural History, The University of Kansas

BY

WILLIAM E. DUELLMAN AND BARBARA BERG

In recent years various museums have issued lists of the type specimens in their collections. These lists are valuable to systematists by providing these workers with information that otherwise sometimes is difficult to obtain. Although by comparison with the large museums in the eastern part of the United States, such as the American Museum of Natural History, the United States National Museum, and the Museum of Comparative Zoology at Harvard, the herpetological collections in the Museum of Natural History at The University of Kansas are relatively small (70,000 specimens), a large number of types are contained in the collection. The largest number of types are of species described from Costa Rica by Edward H. Taylor between 1949 and 1958. Beginning in 1932 and continuing until World War II, Taylor described many species from México; types of these species were contained in the Edward H. Taylor—Hobart M. Smith collection. Inquiries from herpetologists reveal that many workers suppose that the EHT-HMS collection is in the Museum of Natural History. Such is not the case, for the EHT-HMS collection has been divided between the Chicago Natural History Museum and the University of Illinois Museum of Natural History.

The list of type specimens presented here includes all holotypes and paratypes that are known in the museum as of April 15, 1962. Only specimens actually designated as paratypes by the original describer are considered as such. Each species or subspecies is listed in the combination as it was originally proposed. If the name has been subjected to subsequent nomenclatural change or has been placed in synonymy, the name in current use is given after an equals sign, together with a citation to the authority for the change. The arrangement in the following list is alphabetical by genus and species within orders (suborders in the Squamata). Current combinations of names that have been changed subsequent to their original proposal are listed in the correct alphabetical place with a cross-reference to the original combination.

All original citations have been checked, and actual dates of publication are given for each. The checking of original citations, museum catalogues, labels, and sometimes collectors' field catalogues has revealed numerous errors. In some cases the catalogue numbers of the holotypes and paratypes given by Taylor actually were his field numbers. In the following list the museum numbers that were subsequently assigned are given. Certain localities have been given incorrectly; for example, Taylor described several species from Moravia de Chirripó, which he gave as being in Limón Province, Costa Rica. Actually Moravia de Chirripó is in Cartago Province. We have attempted to correct all such errors.

The holotype and two paratypes of *Rana taylori* Smith are stated to be in the Museum of Natural History. Smith (Herpetologica, 15:214, December 8, 1959) proposed the name *Rana taylori* for three specimens discussed by Taylor (Univ. Kansas Sci. Bull., 35:906, July 1, 1952), who gave the numbers 2976-2978. Number 2978 was designated the holotype of *Rana taylori* by Smith, who never saw the frogs. The numbers 2976-2978 are E. H. Taylor's field numbers; the specimens never have been catalogued in the Museum of Natural History, and their present location is unknown.

The 125 species and subspecies represented by holotypes and paratypes in the collection are distributed among the orders of amphibians and reptiles as follows:

AMPHIBIA		REPTILIA	
Gymnophiona (Caecilians)	3	Testudines (Turtles)	5
Caudata (Salamanders)	20	Sauria (Lizards)	31
Salientia (Frogs and Toads)	39	Serpentes (Snakes)	27

GYMNOPHIONA

Dermophis costaricense Taylor, Univ. Kansas Sci. Bull., 37:506, fig. 2, October 15, 1955.

Holotype.—No. 36343, Cinchona, Alajuela Province, Costa Rica; Edward H. Taylor; July 14, 1954.

Paratypes.—Nos. 36337-36340, 36342, 36344-36347, data same as for holotype. Nos. 36447 and 36448, Moravia de Chirripó, Cartago Province, Costa Rica; Edward H. Taylor; August 15-16, 1954.

Dermophis glandulosus Taylor, Univ. Kansas Sci. Bull., 37:509, fig. 3, October 15, 1955.

Holotype.—No. 29979, San Isidro del General, San José Province, Costa Rica; Virgil Cave; 1947.

Dermophis occidentalis Taylor, Univ. Kansas Sci. Bull., 37:503, fig. 1, October 15, 1955.

Holotype.—No. 36298, 15 miles west-southwest of San Isidro del General, San José Province, Costa Rica; Edward H. Taylor; August 3, 1954.

Paratypes.—Nos. 36296 and 36297, same locality; Edward H. Taylor; July 19, 1952.

CAUDATA

Bolitoglossa alvaradoi Taylor, Univ. Kansas Sci. Bull., 36:604, fig. 2, June 1, 1954.

Holotype.—No. 30484, Moravia de Chirripó, Cartago Province, Costa Rica; Edward H. Taylor; August 16, 1951.

Paratypes.—Nos. 34903-34905, same locality; Edward H. Taylor; June 25-26, 1952.

Bolitoglossa arborescandens Taylor, Univ. Kansas Sci. Bull., 36:600, fig. 2, June 1, 1954.

Holotype.—No. 34925, Moravia de Chirripó, Cartago Province, Costa Rica; Edward H. Taylor; August 16, 1951.

Bolitoglossa palustris Taylor, Univ. Kansas Sci. Bull., 33:283, April 20, 1949.

Holotype.—No. 23817, San Isidro del General, San José Province, Costa Rica; Edward H. Taylor; August 23, 1947.

Bolitoglossa veracrucis Taylor, Univ. Kansas Sci. Bull., 34:189, fig. 1, October 1, 1951.

Holotype.—No. 26941, 35 kilometers southeast of Jesús Carranza, Veracruz, México; Walter W. Dalquest; April 6, 1949.

Paratypes.—Nos. 26933-26940, 26942-26953, data same as on holotype.

Chiropterotriton abscondens Taylor, Proc. Biol. Soc. Washington, 61:177, November 12, 1948.

Paratype.—No. 29971, Isla Bonita, Heredia Province, Costa Rica; David Allee and Sr. Machado; August 1, 1947.

Note.—This specimen was listed by Taylor (1948:177) as Richard C. Taylor No. 1416; subsequently the specimen was cataloged as KU 29971.

Magnadigita cerroensis Taylor, Univ. Kansas Sci. Bull., 34:724, pl. 80, February 15, 1952.

Holotype.—No. 29961, Cerro de la Muerte, 2 kilometers below Millville, San José Province, Costa Rica; Edward H. Taylor and Richard C. Taylor; August 15, 1947.

Magnadigita nigrescens Taylor, Univ. Kansas Sci. Bull., 33:282, April 20, 1949.

Holotype.—No. 23816, Boquete Camp, Cerro de la Muerte (on highway between Millville and San Isidro del General), San José Province, Costa Rica; Edward H. Taylor; August 17, 1947.

Magnadigita pesrubra Taylor, Univ. Kansas Sci. Bull., 34:707, pl. 76, text fig. 2, February 15, 1952.

Holotype.—No. 25093, Summit of Cerro de la Muerte, Cartago Province, Costa Rica; Edward H. Taylor and Richard C. Taylor; August 14-15, 1947.

PARATYPES.—(All collected by Edward H. Taylor and Richard C. Taylor in August, 1947) Nos. 25083-25086, 25142-25156, 25157 (166 specimens), Millville, Cerro de la Muerto, San José Province, Costa Rica: Nos. 25082, 25087-25092, 25094-25100, same locality as holotype.

Magnadigita torresi Taylor, Univ. Kansas Sci. Bull., 34:713, pl. 77, February 15, 1952.

HOLOTYPE.—No. 25104, Summit of Cerro de la Muerte, Cartago Province, Costa Rica; Edward H. Taylor and Richard C. Taylor; August 17, 1947.

PARATYPES.—Nos. 25101-25103, 25105-25116, data same as holotype.

NOTE.—Taylor (1952:713) listed 25116a (30 specimens); these are not present in the collection.

Oedipina alleni Taylor, Univ. Kansas Sci. Bull., 36:607, fig. 3, June 1, 1954.

HOLOTYPE.—No. 34926, Palmar, Puntarenas Province, Costa Rica; Edward H. Taylor; September 2, 1952.

Oedipina bonitaensis Taylor, Univ. Kansas Sci. Bull., 34:762, pl. 86, fig. 3, text fig. 8, February 15, 1952.

HOLOTYPE.—No. 29972, Volcán Poás, 6 miles west of Isla Bonita, Alajuela Province, Costa Rica; Edward H. Taylor and Richard C. Taylor; August 3, 1947.

PARATYPES.—Nos. 29973 and 29974, data same as on holotype.

Oedipina cyclocauda Taylor, Univ. Kansas Sci. Bull., 34:764, pl. 87, fig. 4, text fig. 9, February 15, 1952.

HOLOTYPE.—No. 25066, Los Diamantes, 1 kilometer east of Guápiles, Limón Province, Costa Rica; Edward H. Taylor and Richard C. Taylor; September 1-8, 1947.

PARATYPES.—Nos. 25038-25065, data same as on holotype.

Oedipina gracilis Taylor, Univ. Kansas Sci. Bull., 34:773, February 15, 1952.

HOLOTYPE.—No. 29969, Los Diamantes, 1 kilometer east of Guápiles, Limón Province, Costa Rica; Edward H. Taylor and Richard C. Taylor; September 8, 1947.

PARATYPES.—Nos. 29968 and 29970, data same as on holotype.

Oedipina inusitata Taylor, Univ. Kansas Sci. Bull., 34:277, pl. 87, fig. 3, text fig. 13, February 15, 1952.

HOLOTYPE.—No. 29964, 3 miles northeast of Santa Cruz, south slope of Volcán Turrialba, Cartago Province, Costa Rica; Edward H. Taylor; August 9, 1947.

Oedipina longissimus Taylor, Univ. Kansas Sci. Bull., 34:771, pl. 87, fig. 5, text fig. 11, February 15, 1952.

HOLOTYPE.—No. 29963, Cervantes, Cartago Province, Costa Rica; Edward H. Taylor; July 9, 1947.

Oedipina pacificensis Taylor, Univ. Kansas Sci. Bull., 34:775, pl. 87, fig. 2, text fig. 12, February 15, 1952.

HOLOTYPE.—No. 29965, 2 miles east of San Isidro del General, San José Province, Costa Rica; Edward H. Taylor; August 23, 1947.

Oedipina serpens Taylor, Univ. Kansas Sci. Bull., 33:286, April 20, 1949.

HOLOTYPE.—No. 23815, Morehouse Finca, 5 miles southwest of Turrialba, Cartago Province, Costa Rica; Edward H. Taylor; July 2, 1947.

Oedipina syndactyla Taylor, Proc. Biol. Soc. Washington, 61:179, November 12, 1948.

HOLOTYPE.—No. 29962, Volcán Poás, 4 miles west of Isla Bonita, Alajuela Province, Costa Rica; Edward H. Taylor; August 5, 1947.

NOTE.—This specimen was listed by Taylor (1948:179) as No. 843. This is the E. H. Taylor field number; subsequently the specimen was catalogued as KU 29962.

Thorius minutissimus Taylor, Amer. Mus. Novitates, 1437:5, figs. 1-2, December 7, 1949.

PARATYPE.—No. 28080, Santo Tomás Tecpán, Oaxaca, México; Thomas C. MacDougall, 1948.

NOTE.—Received in exchange; formerly this specimen was American Museum of Natural History No. A 53930.

Typhlotriton nereus Bishop, Copeia, 1944(1):1, figs. 1-3, April 21, 1944.

PARATYPES.—Nos. 16036-16038, 16043-16045, near Galena, Cherokee County, Kansas; Wallace Lane and William McNown; March 26, 1932. No. 16199, York Springs, Imboden, Lawrence County, Arkansas; Byron C. Marshall; February, 1930: Nos. 16350, 16352-16354, 16357-16360, near Riverton, Cherokee County, Kansas; Edward H. Taylor; March 26, 1932.

NOTE.—Nos. 16350, 16352-16354, 16357-16360 were listed erroneously by Bishop (1944:1-2) as being from Galena, Cherokee County, Kansas.

SALIENTIA

Agalychnis alcorni Taylor [= *Phyllomedusa dacnicolor* Cope, according to Duellman (Herpetologica, 13:29, 1957)], Copeia, 1952(1):31, figs. 1-2, June 2, 1952.

HOLOTYPE.—No. 29763, South bank of Río Tepalcatepec, 17 miles south of Apatzingán, Michoacán, México; J. R. Alcorn; November 30, 1950.

PARATYPE.—No. 28100, 0.5 miles east of San Blas, Nayarit, México; J. R. Alcorn; January 6, 1949.

Agalychnis saltator Taylor [= *Phyllomedusa saltator* (Taylor), according to Funkhouser (Occas. Papers Nat. Hist. Mus. Stanford Univ., 5:36, 1957)], Univ. Kansas Sci. Bull., 37:527, fig. 10, October 15, 1955.

HOLOTYPE.—No. 35615, Finca Bosco, 5 kilometers north-northeast of Tilarán, Guanacaste Province, Costa Rica; Edward H. Taylor; August 14, 1954.

PARATYPES.—Nos. 35609-10, 35612-35614, 35616-35620, 35622-35626, data same as for holotype.

NOTE.—Taylor (1955:527) erroneously gave the type locality as 4 kilometers north-northeast of Tilarán; in Taylor's field catalogue and in the museum catalogue the locality is listed as 5 kilometers north-northeast of Tilarán. Paratypes 35611 and 35621, listed by Taylor, have been exchanged with the Stanford Natural History Museum.

Atelopus loomisi Taylor—See *Atelopus varius loomis* Taylor.

Atelopus varius loomisi Taylor [= *Atelopus loomisi* Taylor, according to Taylor (Univ. Kansas Sci. Bull., 37:517, 1955)], Univ. Kansas Sci. Bull., 35:625, fig. 7, July 1, 1952.

HOLOTYPE.—No. 24746, Isla Bonita, Heredia Province, Costa Rica; Edward H. Taylor and Richard C. Taylor; June 26, 1947.

PARATYPES.—Nos. 24742-24745, same locality as on holotype, August 1-5, 1947.

Bufo holdridgei Taylor, Univ. Kansas Sci. Bull., 35:607, fig. 3, July 1, 1952.

HOLOTYPE.—No. 30885, Volcán Barba, Heredia Province, Costa Rica; Edward H. Taylor; July 15, 1951.

Centrolenella spinosa Taylor [= *Teratohyla spinosa* (Taylor), according to Taylor (Proc. Biol. Soc. Washington, 64:35, 1951)], Univ. Kansas Sci. Bull., 33:259, April 20, 1949.

HOLOTYPE.—No. 23809, Los Diamantes, 1 kilometer east of Guápiles, Limón Province, Costa Rica; Edward H. Taylor and Richard C. Taylor; September 7, 1947.

PARATYPES.—Nos. 23810-23811, data same as on holotype.

Cochranella albomaculata Taylor, Univ. Kansas Sci. Bull., 33:267, April 20, 1949.

HOLOTYPE.—No. 23814, Los Diamantes, 1 kilometer east of Guápiles, Limón Province, Costa Rica; Edward H. Taylor and Richard C. Taylor; September 7, 1947.

Cochranella chirripoi Taylor, Univ. Kansas Sci. Bull., 39:59, fig. 10, November 18, 1958.

HOLOTYPE.—No. 36865, Cocales Creek, Suretka, Limón Province, Costa Rica; Edward H. Taylor; June 29-30, 1954.

PARATYPES.—Nos. 36862-36864, 36866-36870, data same as on holotype.

Cochranella colymbiphyllum Taylor, Univ. Kansas Sci. Bull., 33:262, April 20, 1949.

HOLOTYPE.—No. 23812, Isla Bonita, Heredia Province, Costa Rica; Edward H. Taylor and Richard C. Taylor; July 29, 1947.

Cochranella decorata Taylor, Univ. Kansas Sci. Bull., 39:50, fig. 6, November 18, 1958.

HOLOTYPE.—No. 36896, Hacienda La Florencia, about 3 miles west of Turrialba, Cartago Province, Costa Rica; Jack Reark; November, 1952.

PARATYPES.—Nos. 36883-36884, San José, San José Province, Costa Rica; Marco Tulio Pacheco; summer, 1954.

NOTE.—The locality of the paratypes is not definite; Taylor presumed that they were from San José. See note under the following species.

Cochranella millepunctata Taylor, Univ. Kansas Sci. Bull., 39:53, fig. 7, November 18, 1958.

HOLOTYPE.—No. 36887, La Palma, San José Province, Costa Rica; Edward H. Taylor, June 20, 1954.

PARATYPES.—No. 32943, Moravia de Chirripó, Cartago Province, Costa Rica; Edward H. Taylor; June 26, 1952. Nos 36885-36886, 36888-36894, data same as holotype. No. 36897, Sarchi, Alajuela Province, Costa Rica; Robert Hunter; summer, 1954.

NOTE.—Taylor (1958:53) erroneously listed 36883 and 36884 as paratypes of this species; on page 50 of the same publication he correctly designated these specimens as paratypes of *Cochranella decorata*. Also, Taylor (1958:53) erroneously listed 32943 as 23943.

Cochranella reticulata Taylor, Univ. Kansas Sci. Bull., 39:61, fig. 11, November 18, 1958.

HOLOTYPE.—No. 32922, Bridge across Río Reventazón, Inter-American Institute of Agriculture, Turrialba, Cartago Province, Costa Rica; Edward H. Taylor; August 1, 1952.

PARATYPES.—No. 32916, Moravia de Chirripó, Cartago Province, Costa Rica; Edward H. Taylor; June 26, 1952. Nos. 32917-32920, Cariblanco, Heredia Province, Costa Rica; Edward H. Taylor; July 20, 1952. No. 32921, data same as holotype. Nos. 32923 and 32924, Palmar, Puntarenas Province, Costa Rica; Edward H. Taylor; September 3, 1952. No. 32925, Golfito, Puntarenas Province, Costa Rica; Edward H. Taylor; September 7, 1952. Nos. 36878-36882, Cocales Creek, Suretka, Limón Province, Costa Rica; Edward H. Taylor; June 30, 1954.

Cochranella talamancae Taylor, Univ. Kansas Sci. Bull., 35:781, 783, July 1, 1952.

HOLOTYPE.—No. 30887, Moravia de Chirripó, Cartago Province, Costa Rica; Edward H. Taylor; August 16, 1951.

NOTE.—Taylor (1952:781) erroneously listed this specimen as KU 4143; actually that is Taylor's field number. Subsequently the specimen was catalogued as KU 30887.

Dendrobates granuliferus Taylor, Univ. Kansas Sci. Bull., 39:10, fig. 5, November 18, 1958.

HOLOTYPE.—No. 43874, Low mountains north of Río Diquis, about 3 miles north of Palmar, Puntarenas Province, Costa Rica; Edward H. Taylor; September 3, 1952.

PARATYPES.—No. 43875, San Isidro del General, San José Province, Costa Rica; Edward H. Taylor; summer, 1952. Nos. 43876-43880, data same as holotype.

NOTE.—Taylor (1958:10) erroneously listed 43875 as being from the type locality.

Eleutherodactylus crassidigitatus Taylor, Univ. Kansas Sci. Bull., 35:740, fig. 31, July 1, 1952.

HOLOTYPE.—No. 28396, Isla Bonita, Heredia Province, Costa Rica; Edward H. Taylor and Richard C. Taylor; July 22-August 3, 1947.

PARATYPES.—Nos. 28360, 28361, 28440, Morehouse Finca, 5 miles southwest of Turrialba, Cartago Province, Costa Rica; Edward H. Taylor and Richard C. Taylor; July 11-21, 1947. Nos. 28362-28368, 28370-28374, data same as on holotype.

NOTE.—Taylor (1952:740) listed 28360, 28361, and 28440 as being from "Turrialba and surroundings."

Eleutherodactylus dubitus Taylor, Univ. Kansas Sci. Bull., 35:707, fig. 22, July 1, 1952.

HOLOTYPE.—No. 24942, Isla Bonita, Heredia Province, Costa Rica; Edward H. Taylor and Richard C. Taylor; July 22-August 3, 1947.

PARATYPES.—Nos. 24910 and 24911, Morehouse Finca, 5 miles southwest of Turrialba, Cartago Province, Costa Rica; Edward H. Taylor and Richard C. Taylor; July 11-16, 1947. Nos. 24912-24914, Santa Cruz Volcán, Cartago Province, Costa Rica; Edward H. Taylor; July 17, 1947. Nos. 24915-24941, 24943-24948, data same as on holotype.

NOTE.—Taylor (1952:707) erroneously listed 24910-24914 as being from the type locality.

Eleutherodactylus minimus Taylor, Univ. Kansas Sci. Bull., 37:517, fig. 7, October 15, 1955.

HOLOTYPE.—No. 37128, 5 kilometers north-northeast of Tilarán, Guanacaste Province, Costa Rica; Edward H. Taylor; August 13, 1954.

PARATYPES.—Nos. 37126, 37127, 37129-37132, data same as on holotype.

Eleutherodactylus persimilis Barbour [= *Microbatrachylus persimilis* (Barbour), according to Taylor (Univ. Kansas Sci. Bull., 35:670, 1952)], Occas. Papers Boston Soc. Nat. Hist., 5:193, pl. 14, January 30, 1926.

PARATYPE.—No. 47166, Suretka, Limón Province, Costa Rica; Emmett R. Dunn and Chester B. Duryea; 1923.

NOTE.—Received in exchange; formerly this specimen was Museum of Comparative Zoology No. 11609.

Eleutherodactylus taurus Taylor, Univ. Kansas Sci. Bull., 39:17, fig. 7, November 18, 1958.

HOLOTYPE.—No. 43866, Golfito, Puntarenas Province, Costa Rica; Edward H. Taylor; September 6, 1952.

PARATYPES.—Nos. 43867, 43869-43871, 43873, same locality as holotype; John Baker and Edward H. Taylor; September 2-6, 1952. Nos. 43868, 43872, Palmar, Puntarenas Province, Costa Rica; Edward H. Taylor; September 2, 1952.

Eleutherodactylus vocator Taylor, Univ. Kansas Sci. Bull., 37:522, fig. 8, October 15, 1955.

HOLOTYPE.—No. 37001, Agua Buena, Puntarenas Province, Costa Rica; Edward H. Taylor; July 25, 1954.

PARATYPES.—Nos. 36999 and 37000, data same as on holotype.

Hyla alvaradoi Taylor, Univ. Kansas Sci. Bull., 35:882, fig. 63, July 1, 1952.

HOLOTYPE.—No. 30886, Moravia de Chirripó, Cartago Province, Costa Rica; Edward H. Taylor; August 16, 1951.

Hyla bivocata Duellman and Hoyt, Copeia, 1961(4):414, figs. 1-3, December 19, 1961.

HOLOTYPE.—No. 58446, 6.2 kilometers by road south of Rayón Mescalapa, Chiapas, México; William E. Duellman and Dale L. Hoyt; August 5, 1960.

PARATYPES.—Nos. 58447-58450, data same as on holotype.

Hyla chaneque Duellman, Herpetologica, 17:1, figs. 1-2, April 15, 1961.

HOLOTYPE.—No. 58439, 6.2 kilometers by road south of Rayón Mescalapa, Chiapas, México; William E. Duellman; August 5, 1960.

PARATYPES.—Nos. 58440-58442, same as holotype. No. 58444, 5.6 kilometers by road south of Rayón Mescalapa, Chiapas, México; William E. Duellman; June 15, 1960.

NOTE.—No. 58443, listed by Duellman (1961:1), has been exchanged with the Museum of Zoology at the University of Michigan.

Hyla cyclomaculata Taylor, Copeia, 1949(4):272, pl. 1, December 15, 1949.

HOLOTYPE.—No. 26954, Huatusco, Veracruz, México; Walter W. Dalquest; December 2, 1948.

Hyla dalquesti Taylor—See *Hyla proboscidea* Taylor.

Hyla debilis Taylor, Univ. Kansas Sci. Bull., 35:880, fig. 62, July 1, 1952.

HOLOTYPE.—No. 28184, Isla Bonita, Heredia Province, Costa Rica; Edward H. Taylor and Richard C. Taylor; August 1, 1947.

Hyla dulcensis Taylor, Univ. Kansas Sci. Bull., 39:37, fig. 17, November 18, 1958.

HOLOTYPE.—No. 32168, Golfito, Puntarenas Province, Costa Rica; Edward H. Taylor; September 7, 1952.

PARATYPES.—Nos. 32166 and 32167, same locality as holotype; John Baker and Edward H. Taylor; September 7 and 8, 1952.

Hyla immensa Taylor, Univ. Kansas Sci. Bull., 35:815,, figs. 42-43, July 1, 1952.

HOLOTYPE.—No. 30404, Inter-American Institute of Agricultural Sciences, Turrialba, Cartago Province, Costa Rica; Edward H. Taylor; June 25, 1951.

Hyla legleri Taylor, Univ. Kansas Sci. Bull., 39:33, figs. 15-16, November 18, 1958.

HOLOTYPE.—No. 32982, 15 kilometers west-southwest of San Isidro General, San José Province, Costa Rica; Edward H. Taylor; July 10, 1952.

PARATYPES.—Nos. 32981, 32983-32988, 35171, same locality as holotype; John Baker and Edward H. Taylor; July 10, 1952.

NOTE.—Taylor (1958:33) erroneously listed 32989-32992 as paratypes of this species; specimens bearing those numbers are *Smilisca gabbi.*

Hyla manisorum Taylor, Univ. Kansas Sci. Bull., 36:630, fig. 11, June 1, 1954.

HOLOTYPE.—No. 34927, Bataan, Limón Province, Costa Rica; Edward H. Taylor; July 22, 1951.

Hyla mixomaculata Taylor, Copeia, 1950(4):274, pl. 1, December 22, 1950.

HOLOTYPE.—No. 26777, Coscomatepec, Veracruz, México; Walter W. Dalquest; December 1, 1948.

PARATYPES.—Nos. 26776, 26778-26780, 26782-26785, data same as on holotype. No. 26781, Huatusco, Veracruz, México; Walter W. Dalquest; December 2, 1948.

NOTE.—Taylor (1950:274) erroneously listed 26786 as a paratype of this species; the specimen bearing that number is a *Hyla staufferi.*

Hyla moraviensis Taylor, Univ. Kansas Sci. Bull., 35:865, fig. 57, July 1, 1952.

HOLOTYPE.—No. 30284, Moravia de Chirripó, Cartago Province, Costa Rica; Edward H. Taylor; August 16, 1951.

PARATYPES.—Nos. 30283, 30285 and 30286, data same as on holotype.

Hyla proboscidea Taylor [= *Hyla dalquesti* Taylor, according to Taylor (Copeia, 1949(1):74, April 15, 1949—substitute name for *Hyla proboscidea* Taylor, preoccupied by *Hyla proboscidea* Brongersma, 1933)], Univ. Kansas Publ. Mus. Nat. Hist., 1:259, figs. a-c, August 16, 1948.

HOLOTYPE.—No. 23626, 2 kilometers west of Jico (= Xico), Veracruz, México; Walter W. Dalquest; October 28, 1946.

PARATYPES.—Nos. 23623-23625, 23627, data same as on holotype.

NOTE.—Taylor (1948:259) erroneously listed 23628 as a paratype of this species; the specimen bearing that number is a *Heloderma suspectum.* However, 23623 not listed by Taylor is a *Hyla proboscidea;* this specimen is noted as a paratype in the museum catalogue.

Hyla rivularis Taylor, Univ. Kansas Sci. Bull., 35:847, fig. 53, July 1, 1952.

HOLOTYPE.—No. 28197, Isla Bonita, Heredia Province, Costa Rica; Edward H. Taylor and Richard C. Taylor; August 1, 1947.

PARATYPES.—Nos. 28196 and 28198, data same as on holotype.

Hyla rufioculis Taylor, Univ. Kansas Sci. Bull., 35:827, fig. 47, July 1, 1952.

HOLOTYPE.—No. 28216, Isla Bonita, Heredia Province, Costa Rica; Edward H. Taylor and Richard C. Taylor; July 28, 1947.

PARATYPES.—Nos. 28204-28210, Morehouse Finca, 5 miles southwest of Turrialba, Cartago Province, Costa Rica; Edward H. Taylor and Richard C. Taylor; July 14, 1947. Nos. 28211-28215, 28217-28222, same locality as holotype; Edward H. Taylor and Richard C. Taylor; July 22-August 3, 1947. Nos. 31072-31078, Moravia de Chirripó, Cartago Province, Costa Rica; Edward H. Taylor; August 16, 1951.

Hyla wellmanorum Taylor [= *Smilisca wellmanorum* (Taylor), according to Starrett (Copeia, 1960(4):303, 1960)], Univ. Kansas Sci. Bull., 35:843, fig. 52, July 1, 1952.

HOLOTYPE.—No. 30302, Bataan, Limón Province, Costa Rica; Edward H. Taylor; July 20, 1951.

PARATYPES.—Nos. 30300 and 30301, data same as on holotype.

Hyla weyerae Taylor, Univ. Kansas Sci. Bull., 36:633, June 1, 1954.

HOLOTYPE.—No. 34850, Esquinas Forest Preserve, Las Esquinas, between Golfito and Palmar, Puntarenas Province, Costa Rica; Mrs. Albert E. Weyer; October, 1952.

Microbatrachylus persimilis (Barbour)—See *Eleutherodactylus persimilis* Barbour.

Microbatrachylus rearki Taylor, Univ. Kansas Sci. Bull., 35:678, fig. 16, July 1, 1952.

HOLOTYPE.—No. 31533, Bataan, Limón Province, Costa Rica; Edward H. Taylor; July 25, 1951.

PARATYPES.—Nos. 30909-30911, 30913, 31539, 31540, 31543-31546, Turrialba, Cartago Province, Costa Rica; Edward H. Taylor; June 26-July 3, 1951. Nos. 30912, 31534-31538, data same as on holotype. Nos. 31541 and 31542, Los Diamantes, 1 kilometer east of Guápiles, Limón Province, Costa Rica; Edward H. Taylor; July 26, 1951.

Plectrohyla brachycephala Taylor [= *Plectrohyla matudai brachycephala* Taylor, according to Bumzahem and Smith (Herpetologica, 10:62, 1954)], Amer. Mus. Novitates, 1437:16, fig. 6, December 7, 1949.

PARATYPE.—No. 28079, Tributary of Río Ostuta, foot of Sierra Madre, between Sierra Madre and Cerro Atravesado, Oaxaca, México; Thomas C. MacDougall; 1948.

NOTE.—Received in exchange; formerly American Museum of Natural History No. A 53758.

Phyllomedusa saltator (Taylor)—See *Agalychnis saltator* Taylor.

Ptychohyla chamulae Duellman, Univ. Kansas Publ. Mus. Nat. Hist., 13:354, pl. 25, fig. 2, April 27, 1961.

HOLOTYPE.—No. 58063, 6.2 kilometers by road south of Rayón Mescalapa, Chiapas, México; William E. Duellman, Dale L. Hoyt, and John Wellman; August 5, 1960.

PARATYPES.—Nos. 58064-58073, data same as on holotype.

Smilisca wellmanorum (Taylor)—See *Hyla wellmanorum* Taylor.

Teratohyla spinosa (Taylor)—See *Centrolenella spinosa* Taylor.

Tomodactylus saxatilis Webb, Univ. Kansas Publ. Mus. Nat. Hist., 15:177, fig. 1, March 7, 1962.

HOLOTYPE.—No. 63326, 8 miles west of El Palmito, Sinaloa, México; Robert G. Webb; June 23, 1961.

PARATYPES.—Nos. 63327-63333, data same as on holotype.

TESTUDINES

Gopherus flavomarginatus Legler, Univ. Kansas Publ. Mus. Nat. Hist., 11: 337, fig. 1, pls. 7-8, April 24, 1959.

PARATYPE.—No. 39415 (carapace only), 8 miles east and 2 miles South of Americanos, Coahuila, México; Robert W. Dickerman; May 19, 1954.

Pseudemys scripta taylori Legler, Univ. Kansas Publ. Mus. Nat. Hist., 13:75, figs. 1-3, pls. 9-12; August 16, 1960.

HOLOTYPE.—No. 46952, 16 kilometers south of Cuatro Ciénegas, Coahuila, México; John M. Legler, September 6, 1958.

PARATYPES.—Nos. 46932-46951, 46953-46969, data same as on holotype. Nos. 46970-46974, 6 miles west of Cuatro Ciénegas, Coahuila, México; John M. Legler; September 3-6, 1958. No. 46976, Río Chiquito, 10 kilometers south of Cuatro Ciénegas; John M. Legler; September 9, 1958.

Trionyx ater Webb and Legler, Univ. Kansas Sci. Bull., 40:21, pls. 1-2, April 20, 1960.

HOLOTYPE.—No. 46903, 16 kilometers south of Cuatro Ciénegas, Coahuila; John M. Legler, Wendell L. Minckley, and Robert B. Wimmer; September 6, 1958.

PARATYPES.—Nos. 46904-46906, 46908-46912, data same as on holotype.

Trionyx muticus calvatus Webb, Univ. Kansas Publ. Mus. Nat. Hist., 11: 519, pls. 13-14, fig. 1, August 14, 1959.

PARATYPES.—Nos. 47117-47119, Pearl River, 1 mile south to 4 miles north of Monticello, Lawrence County, Mississippi; Robert G. Webb; April 10, 1957.

Trionyx spinifera pallidus Webb, Univ. Kansas Publ. Mus. Nat. Hist., 13: 522, pls. 39-40, February 16, 1962.

PARATYPES.—Nos. 2934, 2947, 2966, 2967, 2973, Lewisville, Lafayette County, Arkansas; R. E. McEntyre; May 1, 1926. Nos. 40175 and 40176, Lake Texoma, 2 miles east of Willis, Marshall County, Oklahoma; John M. Legler; summer, 1955. No. 50832, 4 miles southwest of Kingston, Mouth of Caney Creek, Marshall County, Oklahoma; Virgil Dowell; summer, 1954.

SAURIA

Alopoglossus plicatus Taylor [= *Ptychoglossus plicatus* (Taylor), according to Ruibal, Bull. Mus. Comp. Zool., 106:501, 1952)], Univ. Kansas Sci. Bull., 33:272, fig. 1, August 20, 1949.

HOLOTYPE.—No. 23800, Morehouse Finca, 5 miles southwest of Turrialba, Cartago Province, Costa Rica; Edward H. Taylor; July 21, 1947.

Ameiva festiva occidentalis Taylor, Univ. Kansas Sci. Bull., 38:264, fig. 66, December 20, 1956.

PARATYPES.—Nos. 40545-40548, 40553-40558, Agua Buena, Cañas Gordas, Puntarenas Province, Costa Rica; Edward H. Taylor; July 25-26, 1954. Nos. 40549 and 40550, 15 kilometers west-southwest of San Isidro del General, San José Province, Costa Rica; Edward H. Taylor; August 2, 1954.

Anadia metallica arborea Taylor, Univ. Kansas Sci. Bull., 37:542, fig. 13, October 15, 1955.

HOLOTYPE.—No. 34225, Las Flores, Tenoria de Las Cañas, Guanacaste Province, Costa Rica; John Baker and Edward H. Taylor; August 22, 1952.

Anadia metallica attenuata Taylor, Univ. Kansas Sci. Bull., 37:537, fig. 12, October 15, 1955.

HOLOTYPE.—No. 34223, Pacuare, Río Pacuare, Cartago Province, Costa Rica; Edward H. Taylor; August 17, 1951.

PARATYPES.—No. 34224, Moravia de Chirripó, Cartago Province, Costa Rica; Edward H. Taylor; June 26, 1952.

Anolis achilles Taylor, Univ. Kansas Sci. Bull., 38:153, fig. 43, December 20, 1956.

HOLOTYPE.—No. 40634, La Palma, San José Province, Costa Rica; Edward H. Taylor; June 20, 1954.

Anolis allisoni Barbour, Proc. New England Zool. Club, 10:58, July 26, 1928.

PARATYPE.—No. 47167, Coxen Hole, Ruatan Island, Honduras; Thomas Barbour; 1928.

NOTE.—Received in exchange; formerly this specimen was Museum of Comparative Zoology No. 26737.

Anolis aquaticus Taylor, Univ. Kansas Sci. Bull., 38:141, fig. 39, December 20, 1956.

HOLOTYPE.—No. 34276, Palmar, Puntarenas Province, Costa Rica; John Baker; September 3, 1952.

PARATYPES.—Nos. 34277 and 34278, Golfito, Puntarenas Province, Costa Rica; Edward H. Taylor; September 3, 1952.

Anolis biscutiger Taylor, Univ. Kansas Sci. Bull., 38:81, fig. 19, December 20, 1956.

HOLOTYPE.—No. 40771, Golfito, Puntarenas Province, Costa Rica; Edward H. Taylor, September 4-8, 1952.

PARATYPES.—No. 40764, 10-15 kilometers west-southwest of San Isidro del General, San José Province, Costa Rica; Edward H. Taylor; July 10, 1952. Nos. 40766 and 40768, Palmar, Puntarenas Province, Costa Rica; John Baker and Edward H. Taylor; September 2, 1952. Nos. 40769, 40770, 40772-40774, data same as holotype.

NOTES.—Taylor (1956:81) erroneously listed 40769, 40770, 40772-40774 as being from Palmar, instead of Golfito; paratypes 40765 and 40767 have been exchanged with the Museum of Comparative Zoology.

Anolis humilis marsupialis Taylor, Univ. Kansas Sci. Bull., 38:97, fig. 23, December 20, 1956.

HOLOTYPE.—No. 40893, 15 kilometers west-southwest of San Isidro del General, San José Province, Costa Rica; Edward H. Taylor; July 14, 1952.

PARATYPES.—Nos. 40889, 40890, 40892, 40895 and 40896, data same as on holotype.

NOTE.—Paratypes 40891 and 40894 listed by Taylor (1956:97) have been exchanged with the Museum of Comparative Zoology.

Anolis nelsoni Barbour, Mem. Mus. Comp. Zool., Harvard, 44:287, March, 1914.

PARATYPE.—No. 47168, Swan Island, Honduras; George Nelson; March, 1912.

NOTE.—Received in exchange from the Museum of Comparative Zoology.

Anolis woodi attenuatus Taylor, Univ. Kansas Sci. Bull., 38:118, fig. 32, December 20, 1956.

HOLOTYPE.—No. 34257, Isla Bonita, Heredia Province, Costa Rica; Edward H. Taylor; July 29, 1947.

PARATYPE.—No. 34256, data same as holotype.

Aristelliger nelsoni Barbour, Mem. Mus. Comp. Zool., Harvard, 44:258, March, 1914.

Paratype.—No. 47169, Swan Island, Honduras; George Nelson; March, 1912.

NOTE.—Received in exchange; this specimen formerly was Museum of Comparative Zoology No. 9602.

Crotaphytus collaris auriceps Fitch and Tanner, Trans. Kansas Acad. Sci., 54:553, December, 1951.

HOLOTYPE.—No. 29934, 3.5 miles north-northeast of Dewey, west side of Colorado River, Grand County, Utah; Henry S. Fitch; June 28, 1950.

PARATYPES.—Nos. 29935-29942, data same as on holotype.

Eumeces brevirostris bilineatus Tanner, Great Basin Nat., 18:59, fig. 2, November 15, 1958.

HOLOTYPE.—No. 44732, 10 miles southwest of El Salto, Durango, México; Charles M. Fugler; June 28, 1955.

PARATYPES.—Nos. 44728, 44730, 44731, 9 miles southwest of El Salto, Durango, México; Charles M. Fugler and Robert G. Webb; June 26-28, 1955. Nos. 44726, 44729, same locality as holotype; Rollin H. Baker and Robert G. Webb; June 25, 1955. No. 44727, 15 miles southwest of El Salto, Durango, México; Charles M. Fugler; June 25, 1955.

Eumeces dicei pineus Axtell, Copeia, 1960(1):19, figs. 1-2, March 25, 1960.

HOLOTYPE.—No. 39539, Cañon de Carolina, 13 miles east of San Antonio de las Alazanas, Coahuila, México; Robert G. Webb; July 6, 1955.

Eumeces gaigei Taylor [= *Eumeces multivirgatus epipleurotis* Cope, according to Axtell (Texas Jour. Sci., 13:345, 1961)], Univ. Kansas Sci. Bull., 22:219, fig. 1, April 15, 1935.

HOLOTYPE.—No. 7300, near Taos, Taos County, New Mexico; Edward H. Taylor; June 13, 1929.

PARATYPE.—No. 7301, data same as on holotype.

Eumeces inexpectatus Taylor, Univ. Kansas Sci. Bull., 20:251, pls. 17-18, October 1, 1932.

HOLOTYPE.—No. 8232, Citrus County, Florida; Charles E. Burt; March 7, 1930.

Eumeces lynxe durangoensis Tanner, [= *Eumeces lynxe lynxe* (Wiegmann), according to Legler and Webb (Southwest. Nat., 5:16, 1960)], Great Basin Nat., 18:57, fig. 1, November 15, 1958.

HOLOTYPE.—No. 44737, 30 miles east of El Salto, Durango, México; Charles M. Fugler; June 30, 1955.

PARATYPES.—Nos. 44734 and 44735, same as holotype. No. 44736, 10 miles east of El Salto, Durango, México; Charles M. Fugler; June 30, 1955.

Eumeces multivirgatus taylori Smith—See *Eumeces taylori* Smith.

Eumeces taylori Smith [= *Eumeces multivirgatus taylori* Smith, according to Lowe (Herpetologica, 11:233, 1955)], Proc. New England Zool. Club, 21:93, November 14, 1942.

PARATYPE.—No. 13161, Black River, 2 miles east of entrance to Carlsbad Caverns, Eddy County, New Mexico; Edward H. Taylor; September 11, 1931.

Holbrookia bunkeri Smith [= *Holbrookia maculata bunkeri* Smith, according to Williams and Smith (Herpetologica, 13:265, 1958)], Univ. Kansas Sci. Bull., 22:185, April 15, 1935.

HOLOTYPE.—No. 19236, 15 miles south of Juárez, Chihuahua, México; David H. Dunkle and Hobart M. Smith; June 19, 1934.

NOTE.—Formerly this specimen was H. M. Smith No. 80, as given in the original description.

Holbrookia maculata bunkeri Smith—See *Holbrookia bunkeri* Smith.

Leiolopisma cherriei lampropholis Taylor [= *Scincella cherriei lampropholis* (Taylor), according to generic arrangement by Mittleman (Smithsonian Misc. Coll., 117(No. 17):23; 1952)], Univ. Kansas Sci. Bull., 38:287, figs. 71-72, December 20, 1956.

HOLOTYPE.—No. 34436, Bataan, Limón Province, Costa Rica; Edward H. Taylor; July 23-25, 1951.

PARATYPES.—(all from Costa Rica) No. 25169, 5 kilometers southeast of Tilarán, Guanacaste Province; E. Raymond Hall and Marco Tulio Pacheo; March 10, 1947. Nos. 25524-25535, 25538-25542, Interamerican Institute of Agriculture, Turrialba, Cartago Province; Edward H. Taylor and others; June and July, 1947. Nos. 25536 and 25537, Morehouse Finca, 5 miles southwest of Turrialba, Cartago Province; Edward H. Taylor and Richard C. Taylor; July 11-12, 1947. Nos. 34409-34414, Los Diamantes, 1 kilometer east of Guápiles, Limón Province; John Baker and Edward H. Taylor; July and August, 1951. Nos. 34415-34435, 34437 and 34439, data same as on holotype. Nos. 34456-34469, Interamerican Institute of Agriculture, Turrialba, Cartago Province; Edward H. Taylor; July and August, 1951. Nos. 34470-34483, La Lola, Limón Province; John Baker and Edward H. Taylor; August 7-11, 1952. No. 34484, Puerto Limón, Limón Province; Edward H. Taylor; August 3, 1952. No. 34485, Mountain Cow Creek, near Limón, Limón Province; Edward H. Taylor; August 6, 1952. Nos. 34502-34510, Interamerican Institute of Agriculture, Turrialba, Cartago Province; Edward H. Taylor; June, 1952. Nos. 34511-34539, 34864, Interamerican Institute of Agriculture; John Baker and Edward H. Taylor; September, 1952. Nos. 40514-40516, Suretka, Limón Province; Edward H. Taylor; June and July, 1954. No. 40521, Puerto Viejo, Heredia Province; Edward H. Taylor; August 7, 1954.

Lepidophyma anomalum Taylor [= *Lepidophyma obscurum* Barbour, according to Taylor (Univ. Kansas Sci. Bull., 38:220, 1956)], Univ. Kansas Sci. Bull., 37:554, fig. 14, October 15, 1955.

HOLOTYPE.—No. 34207, Los Diamantes, 1 kilometer east of Guápiles, Limón Province, Costa Rica; Edward H. Taylor and Richard C. Taylor; September 3, 1947.

PARATYPES.—Nos. 34205 and 34206, data same as holotype. No. 34208, Morehouse Finca, 5 miles southwest of Turrialba, Cartago Province, Costa Rica; Edward H. Taylor; July 2, 1951. No. 34209, no specific locality in Costa Rica. No. 34210, Bataan, Limón Province, Costa Rica; Edward H. Taylor; July 24, 1951. Nos. 34211, 34212, 34214-34216, La Lola, Limón Province, Costa Rica; John Baker and Edward H. Taylor; August 8-12, 1952. No. 34213, Los Diamantes, 1 kilometer east of Guápiles, Limón Province, Costa Rica; John Baker; August 12, 1952.

Lepidophyma ophiophthalmum Taylor, Univ. Kansas Sci. Bull., 37:558, fig. 15, October 15, 1955.

Holotype.—No. 36250, 5 kilometers north-northeast of Tilarán, Guanacaste Province, Costa Rica; Edward H. Taylor; August 16, 1954.

Paratypes.—Nos. 34217-34219, Las Flores, Tenorio de Las Cañas, Guanacaste Province, Costa Rica; Edward H. Taylor and John Baker; August 22, 1954.

Lepidophyma reticulatum Taylor, Univ. Kansas Sci. Bull., 37:551, fig. 14, October 15, 1955.

Holotype.—No. 36245, Agua Buena, Puntarenas Province, Costa Rica; Edward H. Taylor; July 25, 1954.

Paratypes.—Nos. 34189-34192, 3 kilometers east of San Isidro del General, San José Province, Costa Rica; Edward H. Taylor and Richard C. Taylor; September 1-8, 1947. No. 34193, San Isidro del General, San José Province, Costa Rica; John Baker; July 7, 1952. Nos. 34194-34202, 34204, 15-17 kilometers west-southwest of San Isidro del General, San José Province, Costa Rica; John Baker and Edward H. Taylor; July 10, 1952. Nos. 36230-36237, 4-5 kilometers northwest of Tilarán, Guanacaste Province, Costa Rica; Edward H. Taylor; August 10-15, 1954. Nos. 36238-36244, 36246-36249, data same as on holotype.

Leposoma bisecta Taylor [= *Leposoma southi southi* Ruthven and Gaige, according to Ruibal (Bull. Mus. Comp. Zool., 106:482, 1952)], Univ. Kansas Sci. Bull., 33:275, fig. 2, April 20, 1949.

Holotype.—No. 23801, 0.5 mile west of San Isidro del General, San José Province, Costa Rica; Edward H. Taylor; August 21, 1947.

Leposoma southi orientalis Taylor, Univ. Kansas Sci. Bull., 37:546, October 15, 1955.

Holotype.—No. 36124, Volio, Limón Province, Costa Rica; Edward H. Taylor; June 24, 1954.

Paratype.—No. 36125, same as on holotype.

Mabuya brachypoda Taylor, Univ. Kansas Sci. Bull., 38:308, fig. 76, December 20, 1956.

Holotype.—No. 36258, 4 kilometers east-southeast of Tilarán, Guanacaste Province, Costa Rica; Edward H. Taylor; August 15, 1954.

Paratypes.—Nos. 34310-34313, mouth of Río Barranca, Puntarenas Province, Costa Rica; John Baker and Edward H. Taylor; July 26, 1952. Nos. 34314-34317, Tenorio de Las Cañas, Guanacaste Province, Costa Rica; John Baker and Edward H. Taylor; August 21-24, 1952. No. 34326, Palmar, Puntarenas Province, Costa Rica; Edward H. Taylor; September 2, 1952. Nos. 36312 and 36313, Barranca, Puntarenas Province, Costa Rica; Edward H. Taylor; August 21, 1954.

Mabuya macularia postnasalis Taylor and Elbel, Univ. Kansas Sci. Bull., 38:1105, March 20, 1958.

Holotype.—No. 40110, Phu Lom Lo (mountain), Kok Sathon (village), Dan Sai (district), Loei (province), Thailand; Robert E. Elbel; March 30, 1954.

Paratypes.—Nos. 40109, 40111, 40112, data same as on holotype.

Sceloporus poinsetti macrolepis Smith and Chrapliwy, Herpetologica, 13: 268, January 24, 1958.

PARATYPES.—No. 33855, 4 miles southwest of Coyotes, Durango, México; William M. Lynn; July 14, 1953. Nos. 38097 and 38098, 2 miles west of Sain Alto, Zacatecas, México; Robert W. Dickerman; June 7, 1954.

Scincella cherriei lampropholis (Taylor)—See *Leiolopisma cherriei lampropholis* Taylor.

Urosaurus ornatus caeruleus (Smith)—See *Uta Caerulea* Smith.

Uta caerulea Smith [= *Urosaurus ornatus caeruleus* (Smith), according to Mittleman (Bull. Mus. Comp. Zool., 91:139, 1942)], Univ. Kansas Sci. Bull., 22:172, April 15, 1935.

HOLOTYPE.—No. 19237, about 30 miles north of Ciudad Chihuahua, Chihuahua, México; David H. Dunkle and Hobart M. Smith; June 21, 1934.

PARATYPES.—No. 19238, data same as on holotype. Nos. 19239 and 19240, 20 miles south of Ciudad Chihuahua, Chihuahua, México; David H. Dunkle and Hobart M. Smith; June 21, 1934.

NOTE.—Formerly these specimens were respectively H. M. Smith Nos. 132, 128, 141 and 143, as given in the original description.

Xenosaurus nemanorum Taylor, Univ. Kansas Sci. Bull., 33:183, April 20, 1949.

PARATYPES.—Nos. 24043-24047, Xilitla region, San Luis Potosí, México; Marcella Newman; April 27-June 1, 1947.

NOTE.—Formerly these specimens were respectively Louisiana State University Nos. 502, 496, 492, 503, and 489.

SERPENTES

Bothrops schlegeli supraciliaris Taylor, Univ. Kansas Sci. Bull., 36:791, fig. 39, July 15, 1954.

HOLOTYPE.—No. 31997, mountains near San Isidro del General, San José Province, Costa Rica; collector and date unknown.

Coniophanes fissidens obsoletus Minton and Smith, Herpetologica, 16:108, fig. 1, June 17, 1960.

PARATYPES.—Nos. 30976-30979, 34834, Turrialba, Cartago Province, Costa Rica; John Baker and Edward H. Taylor; June-August, 1951.

Dipsas costaricensis Taylor [= *Sibon longifrenis* (Stejneger), according to Peters (Misc. Publ. Mus. Zool. Univ. Michigan, 114:192, 1960)], Univ. Kansas Sci. Bull., 34:63, pl. 7, fig. 2, October 1, 1951.

HOLOTYPE.—No. 25703, Morehouse Finca, 5 miles southwest of Turrialba, Cartago Province, Costa Rica; Edward H. Taylor; July 16, 1947.

Dipsas tenuissima Taylor, Univ. Kansas Sci. Bull., 36:771, figs. 28-29, July 15, 1954.

HOLOTYPE.—No. 31961, 15 kilometers west-southwest of San Isidro del General, San José Province, Costa Rica; Edward H. Taylor; July 10, 1952.

Dryadophis sanguiventris Taylor, Univ. Kansas Sci. Bull., 36:722, July 15, 1954.

HOLOTYPE.—No. 31978, Esquinas Forest Reserve, Las Esquinas, between Golfito and Palmar, Puntarenas Province, Costa Rica; Edward H. Taylor; September 3, 1952.

Ficimia streckeri Taylor, Copeia, 1931(1):5, March 31, 1931.

HOLOTYPE.—No. 9140, 3 miles east of Rio Grande City, Starr County, Texas; Edward H. Taylor; July 13, 1930.

NOTE.—Taylor (1931:5) erroneously listed the number of the holotype as 4140.

Geophis acutirostris Taylor, Univ. Kansas Sci. Bull., 36:691, fig. 3, July 15, 1954.

HOLOTYPE.—No. 34670, Cot, south slope of Volcán Irazú, Cartago Province, Costa Rica; Edward H. Taylor; July 2, 1952.

Geophis aquilonaris Legler, Univ. Kansas Publ. Mus. Nat. Hist., 11:329, figs. 1-2, January 28, 1959.

HOLOTYPE.—No. 44265, 23 miles south and 1.5 miles east of Creel, Chihuahua, México; Ronald H. Pine; July 23, 1957.

PARATYPE.—No. 44266, data same as on holotype.

Geophis bakeri Taylor, Univ. Kansas Sci. Bull., 36:689, July 15, 1954.

HOLOTYPE.—No. 31983, Isla Bonita, Heredia Province, Costa Rica; Edward H. Taylor; July 19, 1952.

PARATYPES.—No. 30940, Pacayas, Cartago Province, Costa Rica; Edward H. Taylor; August 6, 1951. Nos. 31982, 31984, data same as on holotype.

Geophis zeledoni Taylor, Univ. Kansas Sci. Bull., 36:693, fig. 4, July 15, 1954.

HOLOTYPE.—No. 31992, Finca Zeledon, between Volcán Barba and Volcán Poás, Heredia Province (?), Costa Rica; Edward H. Taylor; July 24, 1952.

PARATYPE.—No. 31951, data same as on holotype.

Lampropeltis doliata taylori Tanner and Loomis, Trans. Kansas Acad. Sci., 60:31, pls. 3-4, April 23, 1957.

PARATYPE.—No. 38952, Vernal, Uintah County, Utah; Lawrence Atwood; 1955.

Lycodon osmanhilli Taylor, Univ. Kansas Sci. Bull., 33:562, pl. 20, March 20, 1950.

HOLOTYPE.—No. 24141, Colombo, Ceylon; W. C. Osman Hill; date unknown.

Micrurus alleni richardi Taylor [= *Micrurus richardi* Taylor, according to Taylor (Univ. Kansas Sci. Bull., 36:777, 1954)], Univ. Kansas Sci. Bull., 34: 169, pl. 23, fig. 7, October 1, 1951.

HOLOTYPE.—No. 25189, Los Diamantes, 1 kilometer east of Guápiles, Limón Province, Costa Rica; Edward H. Taylor and Richard C. Taylor; September 8, 1947.

Micrurus pachecoi Taylor, Univ. Kansas Sci. Bull., 34:165, pl. 22, fig. 6, October 1, 1951.

HOLOTYPE.—No. 25188, Guanacaste Province, Costa Rica; collector and date unknown.

Micrurus richardi Taylor—See *Micrurus alleni richardi* Taylor.

Natrix harteri paucimaculata Tinkle and Conant, Southwestern Naturalist, 6:34 figs. 1-2, June 10, 1961.

PARATYPES.—Nos. 59884 and 59885, Colorado River south of city limits of Robert Lee, Coke County, Texas; Donald W. Tinkle and Don L. McGregor; October 8, 1960.

Natrix rigida sinicola Huheey, Copeia, 1959(4):305, fig. 1, December 30, 1959.

PARATYPE.—No. 24500, Steep Hill Creek, Natchitoches Parish, Louisiana; Henry S. Fitch; August 15, 1947.

Ninia cerroensis Taylor, Univ. Kansas Sci. Bull., 36:699, figs. 5-6, July 15, 1954.

HOLOTYPE.—No. 31935, Pacific slope of Cerro de la Muerte, 7500 feet, San José Province, Costa Rica; Edward H. Taylor; July 8, 1952.

Nothopsis torresi Taylor, Univ. Kansas Sci. Bull., 34:31, pl. 1, October 1, 1951.

HOLOTYPE.—No. 25719, Morehouse Finca, 5 miles southwest of Turrialba, Cartago Province, Costa Rica; Edward H. Taylor; July 16, 1947.

NOTE.—Taylor (1951:31) erroneously listed the number of the holotype as 28719.

Pliocercus annellatus Taylor, Univ. Kansas Sci. Bull., 34:107, pl. 10, fig. 4, October 1, 1951.

HOLOTYPE.—No. 25730, Morehouse Finca, 5 miles southwest of Turrialba, Cartago Province, Costa Rica; Edward H. Taylor; July 11, 1947.

NOTE.—Taylor (1951:107) erroneously listed the number of the holotype as 25370.

Rhadinaea altamontanus Taylor, Univ. Kansas Sci. Bull., 36:740, fig. 16, July 15, 1954.

HOLOTYPE.—No. 30962, National Forest Reserve, Pan-American Highway, Talamanca Range, Cartago Province, Costa Rica; Edward H. Taylor and Jack Reark; August, 1951.

Rhadinaea decipiens rubricollis Taylor, Univ. Kansas Sci. Bull., 36:739, July 15, 1954.

HOLOTYPE.—No. 31956, Cinchona, Alajuela Province, Costa Rica; Edward H. Taylor; June 23, 1952.

Sibynophis collaris triangularis Taylor and Elbel, Univ. Kansas Sci. Bull., 38:1130, fig. 23, March 20, 1958.

HOLOTYPE.—No. 33520, Nongko (village), Siracha (district), Chon Buri (province), Thailand; Boonsong Lekagul; August 18, 1953.

Tantilla costaricensis Taylor [= *Tantilla schistosa costaricensis* Taylor, according to Smith (Herpetologica, 18:16, 1962)], Univ. Kansas Sci. Bull., 36:766, fig. 25a, July 15, 1954.

HOLOTYPE.—No. 30995, Cervantes, Cartago Province, Costa Rica; Edward H. Taylor; August 30, 1951.

Tantilla schistosa costaricensis Taylor—See *Tantilla costaricensis*.

Tantilla schistosa taylori Smith, Herpetologica, 18:17, April 9, 1962.

HOLOTYPE.—No. 35627, Suretka, Limón Province, Costa Rica; Edward H. Taylor; August 1, 1954.

Thamnophis melanogaster chihuahuaensis Tanner, Herpetologica, 15:170, figs. 1-2, December 8, 1959.

PARATYPES.—Nos. 44275-44278, 23 miles south and 1.5 miles east of Creel, Chihuahua, México; Sydney Anderson and Ronald H. Pine; July 19-21, 1957.

NOTE.—Tanner (1959:170) erroneously listed these specimens as being from 1.5 miles east of Creel.

Tropidoclonion lineatum annectens Ramsey, Herpetologica, 9:12, June 1, 1953.

HOLOTYPE.—No. 30005, Tulsa, Tulsa County, Oklahoma; Harold Dundee; May 3, 1951.

PARATYPES.—Nos. 30006-30011, data same as holotype.

Typhlops silus Legler [= *Typhlops lumbricalis* (Linnaeus), according to Richmond (Copeia, 1961(2):222, 1961)], Herpetologica, 15:105, June 2, 1959.

HOLOTYPE.—No. 47469, Banes, Oriente Province, Cuba; Chapman Grant; April, 1956.

PARATYPES.—Nos. 47470 and 47471, data same as on holotype.

Transmitted June 28, 1962.

28-7817

University of Kansas Publications
Museum of Natural History

Volume 15, No. 5, pp. 205-249, pls. 7-10, 6 figs.
October 4, 1963

Amphibians and Reptiles of the Rainforests of Southern El Petén, Guatemala

BY

WILLIAM E. DUELLMAN

University of Kansas
Lawrence
1963

University of Kansas Publications, Museum of Natural History
Editors: E. Raymond Hall, Chairman, Henry S. Fitch,
Theodore H. Eaton, Jr.

Vol. 15, No. 5, pp. 205-249, pls. 7-10, 6 figs.
Published October 4, 1963

University of Kansas
Lawrence, Kansas

NOV 11 1963
UNIVERSITY

PRINTED BY
JEAN M. NEIBARGER, STATE PRINTER
TOPEKA, KANSAS
1963
29-5935

Amphibians and Reptiles of the Rainforests of Southern El Petén, Guatemala

BY

WILLIAM E. DUELLMAN

CONTENTS

PAGE

Introduction 207
Acknowledgments 208
Description of Area 208
Physiography 209
Climate 209
Vegetation 209
Gazetteer 210
The Herpetofauna of the Rainforest 211
Composition of the Fauna 212
Ecology of the Herpetofauna 212
Relationships of the Fauna 217
Accounts of Species 218
Hypothetical List of Species 246
Summary 247
Literature Cited 247

INTRODUCTION

Early in 1960 an unusual opportunity arose to carry on biological field work in the midst of virgin rainforest in southern El Petén, Guatemala. At that time the Ohio Oil Company of Guatemala had an air strip and camp at Chinajá, from which place the company was constructing a road northward through the forest. In mid-February, 1960, J. Knox Jones, Jr. and I flew into El Petén to collect and study mammals, reptiles, and amphibians. While enjoying the comforts of the fine field camp at Chinajá, we worked in the surrounding forest and availed ourselves of the opportunity to be on hand when the road crews were cutting the tall trees in the forest, thereby bringing to the ground many interesting specimens of the arboreal fauna. We stayed at Chinajá until late March, with the exception of a week spent at Toocog, another camp of the Ohio Oil Company located 15 kilometers southeast of La Libertad and on the edge of the savanna. Thus, at Toocog we were able

to work both in the forest and on the savanna. In the summer of 1960, John Wellman accompanied me to El Petén for two weeks in June and July. Most of our time was spent at Chinajá, but a few days were spent at Toocog and other localities in south-central El Petén.

Many areas in Guatemala have been studied intensively by L. C. Stuart, who has published on the herpetofauna of the forested area of northeastern El Petén (1958), the savannas of central El Petén (1935), and the humid mountainous region to the south of El Petén in Alta Verapaz (1948 and 1950). The area studied by me and my companions is covered with rainforest and lies to the north of the highlands of Alta Verapaz and to the south of the savannas of central El Petén. A few specimens of amphibians and reptiles were obtained in this area in 1935 by C. L. Hubbs and Henry van der Schalie; this collection, reported on by Stuart (1937), contained only one species, *Cochranella fleishmanni*, not present in our collection of 77 species and 617 specimens.

Acknowledgments

I am grateful to L. C. Stuart of the University of Michigan, who made the initial arrangements for our work in El Petén, aided me in the identification of certain specimens, and helped in the preparation of this report. J. Knox Jones, Jr. and John Wellman were able field companions, who added greatly to the number of specimens in the collection. In Guatemala, Clark M. Shimeall and Harold Hoopman of the Ohio Oil Company of Guatemala made available to us the facilities of the company's camps at Chinajá and Toocog. Alberto Alcain and Luis Escaler welcomed us at Chinajá and gave us every possible assistance. Juan Monteras and Antonio Aldaña made our stay at Toocog enjoyable and profitable. During our visits to southern El Petén, Julio Bolón C. worked for us as a collector, and between March and June he collected and saved many valuable specimens; his knowledge of the forest and its inhabitants was a great asset to our work. Jorge A. Ibarra, Director of the Museo Nacional de Historia Natural in Guatemala assisted us in obtaining necessary permits and extended other kindnesses. To all of these people I am indebted for the essential parts that they played in the completion of this study.

Field work in the winter of 1960 was made possible by funds from the American Heart Association for the purposes of collecting mammalian hearts. My field work in the summer of 1960 was supported by a grant from the Graduate Research Fund of the University of Kansas.

DESCRIPTION OF THE AREA

A vast lowland region stretches northward for approximately 700 kilometers from the highlands of Guatemala to the Gulf of Mexico. The northern two-thirds of this low plain is bordered on three sides by seas and forms the Yucatan Peninsula. The lowlands

at the base of the Yucatan Peninsula make up the Departamento El Petén of Guatemala. The area with which this report is concerned consists of the south-central part of El Petén.

Physiography

Immediately south of Chinajá is a range of hills, the Serrania de Chinajá, having an almost due east-west axis and a crest of about 600 meters above sea level. South of the Serrania de Chinajá are succeedingly higher ridges building up to the Meseta de Cobán and Sierra de Pocolha and eventually to the main Guatemalan highlands. The northern face of the Serrania de Chinajá is a fault scarp dropping abruptly from about 650 meters at the crest to about 140 meters at the base. From the base of the Serrania de Chinajá northward to the Río de la Pasión at Sayaxché the terrain is gently rolling and has a total relief of about 50 meters. North of the Río de la Pasión is a low dome reaching an elevation of 170 meters at La Libertad; see Stuart (1935:12) for further discussion of the physiography of central El Petén. The rocks in southern El Petén are predominately Miocene marine limestones; there are occasional pockets of Pliocene deposits. There is little evidence of subterranean solution at Chinajá, but northward in central El Petén karsting is common. The upper few inches of soil is humus rich in organic matter; below this is clay.

Climate

The climate of El Petén is tropical with equable temperatures throughout the year. Temperatures at Chinajá varied between a night-time low of 65° F. and a daytime high of 91° F. during the time of our visits. In the Köppen system of classification the climate at Chinajá and Toocog is Af. Rain falls throughout the year, but there is a noticeable dry season. To anyone who has traveled from south to north in El Petén and the Yucatan Peninsula, it is obvious from the changes in vegetation that there is a decrease in rainfall from south to north. There is a noticeable difference between Chinajá and Toocog. Although rainfall data are not available for Chinajá and Toocog, there are records for nearby stations (Sapper, 1932). At Paso Caballos on the Río San Pedro about 40 kilometers northwest of Toocog the average annual rainfall amounts to 1620 mm.; the driest month is March (21 mm.), and the wettest months are June (269 mm.) and September (265 mm.). At Cubiquitz, Alta Verapez, about 35 kilometers south-southwest of Chinajá and at an elevation of 300 meters, the average annual rainfall is 4006 mm.; the driest month is March (128 mm.), and the wettest months are July (488 mm.) and October (634 mm.).

During the 18 days in February and March, 1960, that we kept records on the weather at Chinajá moderate to heavy showers occurred on seven days. During our stay there in June and July rain fell every day, as it did in Toocog. However, during the week spent at Toocog in March no rain fell.

Vegetation

The vegetation of northern and central El Petén has been studied by Lundell (1937), who made only passing remarks concerning the plants of the southern part of El Petén. No floristic studies have been made there. The

following remarks are necessarily brief and are intended only to give the reader a general picture of the forest. I have included names of a few of the commoner trees that I recognized.

Chinajá is located in a vast expanse of unbroken rainforest. In this forest there is a noticeable stratification of the vegetation. Three strata are apparent; in the uppermost layer the tops of the trees are from 40 to 50 meters above the ground. The spreading crowns of the trees and the interlacing vines form a nearly continuous canopy over the lower layers. Among the common trees in the upper stratum are *Calophyllum brasiliense, Castilla elastica, Cedrela mexicana, Ceiba pentandra, Didalium guianense, Ficus* sp., *Sideroxylon lundelli, Swietenia macrophylla,* and *Vitex* sp. (Pl. 1, fig. 1). The middle layer of trees have crowns about 25 meters above the ground; these trees in some places where the upper canopy is missing form the tallest trees in the forest. This is especially true on steep hillsides. Common trees in the middle layer include *Achras zapote, Bombax ellipticum, Cecropia mexicana, Orbignya cohune,* and *Sabal* sp. The lowermost layer reaches a height of about 10 meters; in many places in the forest this layer is absent. Common trees in the lower stratum include *Crysophila argentea, Cymbopetalum penduliflorum, Cascaria* sp., and *Hasseltia dioica.*

The ground cover is sparce; apparently only a few small herbs and ferns live on the heavily shaded forest floor. Important herpetological habitats include the leaf litter, rotting stumps, and rotting tree trunks on the forest floor and the buttresses of many of the gigantic trees, especially *Ceiba pentandra* (Pl. 2). Epiphytes, especially various kinds of bromeliads, are common. Most frequently these are in the trees in the upper and middle strata.

At Toocog there is sharp break between savanna and forest (Pl. 7, fig. 2). The forest is noticeably drier and more open than at Chinajá (Pl. 9). The crowns of the trees are lower, and there is no nearly continuous canopy between 40 and 50 meters above the ground. Although *Swietenia macrophylla* and other large trees occur, they are less common than at Chinajá. Especially common at Toocog are *Achras zapote, Brosimum alicastrum,* and various species of *Ficus.*

GAZETTEER

The localities from which specimens were obtained are cited below and shown on the accompanying map (Fig. 1).

Chinajá.—Lat. 16° 02′, long. 90° 13′, elev. 140 m. Camp of the Ohio Oil Company of Guatemala and formerly a small settlement. On some maps Chinajá is located just to the north of the Alta Verapaz—El Petén boundary; recent surveys place the location just to the south of the imaginary line through the rainforest. Field work was conducted in the immediate vicinity of the camp, on the lower slopes of the Serrania de Chinajá, and at several sites to the northwest and north-northwest of Chinajá, where the forest was being cleared. The entire area supports rainforest.

La Libertad.—Lat. 16° 47′, long. 90° 07′, elev., 170 m. A town on the savannas in central El Petén; although we collected there in the rainy season, the specimens obtained on the savannas are not included in this report.

Paso Subín.—Lat. 16° 38′, long. 90° 12′, elev. 90 m. A small settlement on the Río Subín, a tributary of the Río de la Pasión. Specimens were obtained in rainforest in the immediate vicinity of the settlement.

Río de la Pasión.—A large river flowing northward through southern El Petén and thence westward into the Río Usumacinta. Specimens were obtained along the river between the Río Subín and Sayaxché.

FIG. 1. Map of El Petén, Guatemala, showing localities mentioned in text.

Río San Román.—A river flowing northward in south-central El Petén to the Río Salinas (Usumacinta). We collected along the river at a place about 16 kilometers north-northwest of Chinajá, approximately at Lat. 16° 10′, long. 90° 17′, elev. 110 m. In the dry reason the river was clear; it is surrounded by rainforest.

Sayaxché.—Lat. 16° 31′, long. 90° 09′, elev. 80 m. A town on the southern bank of the Río de la Pasión. Specimens were obtained in the rainforest and in cleared areas in the immediate vicinity of the town.

Toocog (formerly Sojío).—Lat. 16° 41′, long. 90° 02′, elev. 140 m. A camp of the Ohio Oil Company of Guatemala located at the rainforest-savanna edge, 15 kilometers southeast of La Libertad. Although we collected on the savannas as well as in the forest, especially to the east of the camp, only species obtained in the forest are considered in this report.

THE HERPETOFAUNA OF THE RAINFOREST

In presenting an account of the herpetofauna of southern El Petén three items need to be considered: (1) The composition of the fauna; (2) the ecology of the fauna; (3) the relationships of the fauna. Each of these topics is discussed briefly below. Logically a discussion of the origin of the fauna should follow, but this is being withheld for inclusion in a report on the herpetofauna of the entire El Petén by L. C. Stuart and the author; at that time the above topics will be expanded to cover the herpetofauna of the whole region.

Composition of the Fauna

A total of 78 species of amphibians and reptiles has been found in the rainforests in southern El Petén; a break down into families and genera is given in table 1. Another 13 species probably occur in southern El Petén (see

TABLE 1.—COMPOSITION OF THE HERPETOFAUNA IN SOUTHERN EL PETÉN, GUATEMALA.

Group	Families	Genera	Species
Gymnophiona	(1)*	(1)	(1)
Caudata	1	1	2
Salientia	6	10 (1)	19 (1)
Crocodilia	1	1	1
Testudines	4	7	8
Sauria	6	13 (1)	19 (1)
Serpentes	4	21 (7)	29 (10)
Total	22 (1)	53 (10)	78 (13)

* Numbers in parenthesis indicate the number of additional taxa that probably occur.

Hypothetical List of Species). The fauna primarily is composed of typical humid lowland forest inhabitants, such as:

Hyla ebraccata
Hyla loquax
Phyllomedusa callidryas taylori
Smilisca phaeota cyanosticta
Anolis biporcatus
Anolis capito
Anolis humilis uniformis
Eumeces sumichrasti
Ameiva festiva edwardsi
Imantodes cenchoa leucomelas
Leptophis ahuetulla praestans
Xenodon rabdocephalus mexicanus
Bothrops nasutus
Bothrops schlegeli schlegeli

Nevertheless, the region also provides at least a limited amount of habitat suitable for some species that are more frequently found in open forest of a drier nature; such species include:

Hyla microcephala martini
Hyla staufferi
Hypopachus cuneus nigroreticulatus
Anolis sericeus sericeus
Eumeces schwartzei
Oxybelis aeneus aeneus

Because of the absence of sufficiently open habitat or owing to the presence of competitors, some conspicuous members of sub-humid forests are not present in southern El Petén. Conspicuous absentees are the following:

Rhinophrynus dorsalis
Phrynohyas spilomma
Triprion petasatus
Anolis tropidonotus
Ctenosaura similis
Ameiva undulata
Cnemidophorus angusticeps
Conophis lineatus
Masticophis mentovarius mentovarius

Ecology of the Herpetofauna

Our two visits to Chinajá and Toocog afforded the opportunity to gather data on the ecology of the rainforests of southern El Petén and to study the relationships between the environment and members of the herpetofauna. Tropical rainforests present the opti-

FIG. 1. Edge of rainforest along airstrip at Chinajá, El Petén, Guatemala.

FIG. 2. Rainforest at edge of savanna at Toocog, El Petén, Guatemala.

PLATE 8

Interior of rainforest at Chinajá. Notice size of buttresses on large tree (*Ceiba pentandra*).

PLATE 9

Interior of rainforest at Toocog. Notice less dense vegetation as compared with Pl. 8.

FIG. 1. Rainforest along Río San Román, 16 kilometers north-northwest of Chinajá.

FIG. 2. Rain pond in forest at Toocog. This was a breeding site for six species of frogs.

mum conditions for life, and it is in this environment that life reaches its greatest diversity. Here, too, biological inter-relationships are most complex. This complexity is illustrated by the presence of many species of some genera, all of which are found together in the same geographic region. In the rainforests of southern El Petén there are six species of *Anolis,* five of *Hyla,* four of *Bothrops,* and three of *Coniophanes.* Obviously, the diversity of ecological niches in the rainforest is sufficient to support a variety of related species. Of the examples mentioned above, fairly adequate ecological data were obtained for most of the species of *Anolis,* which will be used to show the ecological diversity and vertical stratification of sympatric species in the rainforests.

Of the six species of *Anolis,* all except *A. sericeus* are typically found in humid forests. *Anolis sericeus sericeus* is poorly represented in the collections from southern El Petén, where it may be in competition with *Anolis limifrons rodriguezi* that resembles *Anolis s. sericeus* in size, coloration, and habits. Therefore, *Anolis sericeus sericeus* is excluded from the following discussion. The common terrestrial species is *Anolis humilis uniformis;* sometimes this small species perches or suns on the bases of small trees or buttresses of some large trees. When disturbed it takes to the ground and seeks cover in the leaf litter or beneath logs or palm fronds. *Anolis lemurinus bourgeaei* is about twice the size of *Anolis humilis uniformis* and is usually observed on buttresses of large trees or on the lower two meters of tree trunks. Individuals were seen foraging on the ground along with *Anolis humilis uniformis.* At no time were *Anolis lemurinus bourgeaei* observed to ascend the trunks of large trees; they always took refuge near the bases of trees. *Anolis limifrons rodriguezi* is found on the stems and branches of bushes. It is a small species that sometimes is observed on the ground but was never seen ascending large trees. *Anolis capito* is about the same size as *Anolis lemurinus bourgeaei* and lives on the trunks of large trees. In the tops of the trees lives a large green species, *Anolis biporcatus.*

Similar segregation habitatwise can be demonstrated for other members of the herpetofauna. The avoidance of interspecific competition in feeding is well illustrated by three species of snakes that probably are the primary ophidian predators on frogs. *Drymobius margaritiferus margaritiferus* is diurnal and terrestrial; it feeds on frogs at the edges of breeding ponds by day. Also during the day *Leptophis mexicanus mexicanus* feeds on frogs in

bushes and trees. At night the activities of both of these species is replaced by those of *Leptodeira septentrionalis polysticta*, which not only feeds on the frogs in the trees and bushes, but descends to the ground and even enters the water in search of food.

From the examples discussed above, the importance of the three dimensional aspect of the rainforest is apparent. The presence of a large and diverse habitat above the ground is of great significance in the rainforest, for of the non-aquatic components of the herpetofauna in the rainforests of southern El Petén, 42 per cent of the species spend at least part of their lives in the bushes and trees. Another important part of the forest is the subterranean level—the rich mulch, underground tunnels, and rotting subterranean vegetation. Of the 78 species of amphibians and reptiles in southern El Petén, seven are primarily fossorial, and half-a-dozen others are secondarily fossorial. Probably the fossorial members of the fauna are the least well represented in the collection, for such widespread species as *Dermophis mexicanus mexicanus*, *Rhadinaea decorata decorata* and *Tantilla schistosa schistosa* were expected, but not found.

In the following discussion of the ecological distribution of amphibians and reptiles in the rainforest I have depended chiefly on my observations made in southern El Petén, but have taken into consideration observations made on the same species in other regions, together with reports from other workers. The reader should keep in mind that the evidence varies from species to species. Of some species I have observed only one animal in the field; of others, I have seen scores and sometimes hundreds of individuals. For species on which I have few observations or rather inconclusive evidence, the circumstance of inadequate data is mentioned.

In analyzing the ecological distribution within the forest, it is convenient to recognize five subdivisions (habitats); each is treated below as a unit.

1. Aquatic.—This habitat includes permanent streams and rivers (Pl. 10, fig. 1), some of which are clear and others muddy. In the rainy season temporary ponds form in depressions on the forest floor (Pl. 10, fig. 2); these are important as breeding sites for many species of amphibians. Aquatic members of the herpetofauna are here considered to be those species that either spend the greatest part of their lives in the water or usually retreat to water for shelter. Seven species of turtles and one crocodilian are

aquatic. Of these, *Dermatemys mawi, Staurotypus triporcatus,* and *Pseudemys scripta ornata* inhabit clear water, whereas *Chelydra rossignoni, Claudius angustatus, Kinosternon acutum,* and *K. leucostomum* inhabit muddy water. *Crocodylus moreleti* apparently inhabits both clear and muddy water, for in the dry season it lives along the clear rivers, but in the rainy season inhabits flooded areas in the forest as well.

2. AQUATIC MARGIN.—Extensive marshes were lacking in the part of southern El Petén that I visited; consequently, the aquatic margin habitat is there limited to the edges of rivers and borders of temporary ponds. *Bufo marinus, Rana palmipes,* and *Rana pipiens* are characteristic inhabitants of the aquatic margin, although in the rainy reason *Bufo marinus* often is found away from water. Observations indicate that *Tretanorhinus nigroluteus lateralis* inhabits the margins of ponds and streams and actually spends considerable time in the water. Although *Iguana iguana rhinolopha* is arboreal, it lives in trees along rivers, into which it plunges upon being disturbed. Species included in this category are those that customarily spend most of their lives at the edge of permanent water. Frogs and toads that migrate to the water for breeding and the snakes that prey on the frogs at that time are not assigned to the aquatic-margin habitat.

3. FOSSORIAL.—Characteristic inhabitants of the mulch on the forest floor are *Bolitoglossa moreleti mulleri, Lepidophyma flavimaculatum flavimaculatum, Scincella cherriei cherriei, Ninia sebae sebae, Pliocercus euryzonus aequalis,* and *Micrurus affinis apiatus.* Other species of snakes that spend most of their lives above ground often forage in the mulch layer; among these are *Coniophanes bipunctatus biserialis, Coniophanes fissidens fissidens, Coniophanes imperialis clavatus, Lampropeltis doliata polyzona,* and *Stenorrhina degenhardti.* Among the amphibians, at least *Hypopachus cuneus nigroreticulatus, Eleutherodactylus rostralis,* and *Syrrhophus leprus* are known to seek shelter in the mulch.

4. TERRESTRIAL.—One turtle, *Geoemyda areolata,* is primarly terrestrial. Among the lizards, conspicuous terrestrial species are *Anolis humilis uniformis* and *Ameiva festiva edwardsi; Anolis lemurinus bourgeaei* and *Basiliscus vittatus* spend part of their lives on the ground, but also live on trees and in bushes. *Eumeces schwartzei* and *E. sumichrasti* apparently are terrestrial. The only terrestrial lizard that is nocturnal is *Coleonyx elegans elegans,* which

by day hides in the leaf litter or below ground. Nocturnal amphibians that are terrestrial include *Bufo marinus, Bufo valliceps valliceps, Eleutherodactylus rugulosus rugulosus, Syrrhophus leprus,* and *Hypopachus cuneus nigroreticulatus.* A large number of active diurnal snakes are terrestrial; these include *Boa constrictor imperator, Clelia clelia clelia, Dryadophis melanolomus laevis, Drymarchon corais melanurus, Drymobius margaritiferus margaritiferus, Pseustes poecilonotus poecilonotus,* and *Spilotes pullatus mexicanus.* Nocturnal terrestrial snakes include three kinds of *Bothrops* (*B. atrox asper, B. nasutus,* and *B. nummifer nummifer*), all of which seem to be equally active by day.

5. ARBOREAL.—In this habitat the third dimension (height) of the rainforest probably is the most complex insofar as the interrelationships of species and ecological niches are concerned. I have attempted to categorize species as to microhabitats within the arboreal habitat; in so doing, I recognize four subdivisions—bushes, tree trunks, tree tops, and epiphytes.

Bush inhabitants include several species of lizards and snakes, all of which have rather elongate, slender bodies, and long tails. Common bush-inhabitants in southern El Petén are *Anolis limifrons rodriguezi, Basiliscus vittatus, Laemanctus deborrei, Leptophis mexicanus mexicanus,* and *Oxybelis aeneus aeneus.* All of these are diurnal, and all but *Laemanctus* have been observed sleeping on bushes at night.

Tree-trunk inhabitants include five species of lizards. *Thecadactylus rapicaudus* lives on the trunks of large trees; *Sphaerodactylus lineolatus* lives beneath the bark on dead trees and on corozo palms. *Anolis lemurinus bourgeaei* lives on the bases and butresses of large trees, from which it often descends to the ground. *Corythophanes cristatus* and *Anolis capito* were found only on tree trunks and large vines.

The least information is available for the species living in the tree tops. The following species were obtained from tops of trees when they were felled, or have been observed living in the tree tops: *Anolis biporcatus, Iguana iguana rhinolopha, Celestus rozellae, Leptodeira septentrionalis polysticta, Leptophis ahaetulla praestans, Sibon dimidiata dimidiata,* and *Sibon nebulata nebulata.*

Epiphytes, especially the bromeliads, provide refuge for a variety of tree frogs and small snakes. Of the tree frogs, *Hyla picta, Hyla staufferi, Phyllomedusa callidryas taylori, Similisca baudini,* and *Similisca phaeota cyanosticta* have been found in bromeliads; other

species probably occur there. Among the snakes, *Imantodes cenchoa leucomelas, Leptodeira frenata malleisi, Leptodeira septentrionalis polysticta, Sibon dimidiata dimidiata,* and *Sibon nebulata nebulata* are frequent inhabitants of bromeliads; all of these snakes are nocturnal.

Relationships of the Fauna

Most of the 78 species of amphibians and reptiles definitely known from the rainforest in southern El Petén have extensive ranges in the Atlantic lowlands of southern México and Central America; many extend into South America. Sixty-two (80%) of the species belong to this group having extensive ranges in Middle America. Three species (*Syrrhophus leprus, Leptodeira frenata,* and *Kinosternon acutum*) are at the southern limits of their distributions in southern El Petén and northern Alta Verapaz, whereas *Eleutherodactylus rostralis* and *Thecadactylus rapicaudus* are at the northern and western limits of their distributions in El Petén. Nine (11%) species have the center of their distributions in El Petén and the Yucatan Peninsula; representatives of this group include *Claudius angustatus, Dermatemys mawi, Laemanctus deborrei,* and *Eumeces schwartzei.*

In determining a measure of faunal resemblance, I have departed from the formulae discussed by Simpson (1960) and have analyzed the degree of resemblance by the following formula used to calculate an index of faunal relationships:

$$\frac{C\ (2)}{N_1 + N_2} = R, \text{ where}$$

C = species common to both faunas.
N_1 = number of species in the first fauna.
N_2 = number of species in the second fauna.
R = degree of relationships (when R = 1.00, the faunas are identical; when R = 0, the faunas are completely different).

The herpetofauna of southern El Petén has been compared with that in the Tikal-Uaxactún area (Stuart, 1958), that in the humid lowlands of Alta Verapaz (Stuart, 1950, plus additional data), and that in the Mexican state of Yucatán (Smith and Taylor, 1945, 1948, and 1950). The herpetofaunas of lowland Alta Verapaz and Yucatán are the largest, having respectively 94 and 91 species, where as there are 78 species known from southern El Petén and 64 from the Tikal-Uaxactún area. An analysis of faunal relationships (Table 2) shows that the faunas of the rainforests of southern El Petén and lowland Alta Verapaz are closely related. The relationships between these two areas and the Tikal-Uaxactún area

TABLE 2.—INDEX OF FAUNAL RELATIONSHIPS BETWEEN SOUTHERN EL PETÉN AND OTHER REGIONS.

	Lowland Alta Verapaz	Southern El Petén	Tikal-Uaxactún Area	Yucatán
Lowland Alta Verapaz	.....	.85	.61	.43
Southern El Petén	.85	.....	.64	.41
Tikal-Uaxactún Area	.61	.64	.....	.63
Yucatán	.43	.41	.63	.....

in northern El Petén is notably less. Apparently the biggest faunal changes take place between southern El Petén and the Tikal-Uaxactún area, and between the latter and Yucatán. As stated by Stuart (1958:7) the Tikal-Uaxactún is transitional between the humid rainforests to the south and the dry outer end of the Yucatan Peninsula. The transitional nature of the environment is exemplified by a rather depauperate herpetofauna consisting of some species of both dry and humid environments and lacking a large fauna typical of either. Contrariwise, the continuity of the environment from southern El Petén to the lowlands of Alta Verapaz is reflected in degree of resemblance of the herpetofaunas.

Most of the species of amphibians and reptiles found in southern El Petén are found in humid tropical forests from the Isthmus of Tehuantepec southeastward on the Atlantic lowlands well into Central America.

ACCOUNTS OF SPECIES

In the following pages various aspects of the occurrence, life histories, ecology, and variation of the species of amphibians and reptiles known from southern El Petén are discussed. Only *Cochranella fleischmanni* reported by Stuart (1937) from Rió Subín at Santa Teresa was not collected by us and is excluded. Because more worthwhile information was gathered for some species than others, the length and completeness of the accounts vary. All specimens listed are in the Museum of Natural History at the University of Kansas, to which institution all catalog numbers refer. Preceding the discussion of each species is an alphabetical list of

localities from which specimens were obtained; numbers after a locality indicate the number of specimens obtained at each locality.

Bolitoglossa dofleini (Werner)

Chinajá, 1.

An adult female having minute ovarian eggs has a snout-vent length of 81 mm., a tail length of 59 mm., 13 costal grooves, two intercostal spaces between adpressed toes, 38-35 vomerine teeth in irregular rows forming a broad arch from a point posterolaterad to the internal nares to a point near the anterior edge of the parasphenoid teeth, and 43-44 maxilliary-premaxillary teeth. In life the dorsum was rusty brown with irregular black and orange spots and streaks. The flanks were bluish gray with black in the costal grooves and creamy tan flecks along the ventral edge of the flank. The belly and underside of the tail were yellowish tan with dark brown spots laterally. The limbs were orange proximally and black distally; the pads of the feet were bluish black. The dorsal and lateral surfaces of the tail were yellowish orange with black spots. The iris was grayish yellow.

Stuart (1943:17) reported this species from Finca Volcán, Alta Verapaz. He diagnosed his specimens as having 13 costal grooves and two or three intercostal spaces between adpressed toes. He stated that the vomerine teeth were about 12 in number and that in life the dorsum was mottled gray and black, the sides gray and brown, and the undersurfaces uniformly dark gray. These specimens differ noticeably from the individual from Chinajá in the number of vomerine teeth and in coloration.

In August, 1961, I obtained a specimen of *Bolitoglossa dofleini* at Finca Los Alpes, Alta Verapaz, approximately 13 kilometers airline south-southwest of Finca Volcán and at approximately the same elevation. Although the salamander was dead when found, it obviously was more heavily pigmented than the individual from Chinajá. The belly was bluish gray with black spots laterally; the dorsum was dull brownish gray with some brownish red streaks. The specimen is a female having small ovarian eggs, a snout-vent length of 90 mm., 13 costal grooves, and two intercostal spaces between adpressed limbs. There are 28-29 vomerine teeth, more than twice as many as in specimens from Finca Volcán (Stuart, 1943:17), but noticeably fewer than in the specimen from Chinajá.

The presence of this species at Chinajá lends support to the idea that the specimen from the Río de la Pasión listed by Brocchi

(1882:116) also is *Bolitoglossa dofleini.* Furthermore, the confirmed presence of this species in the lowlands of El Petén suggests that there may be genetic connection between *B. dofleini* in the Alta Verapaz and *B. yucatana* in the Yucatan Peninsula. *Bolitoglossa yucatana* differs from *B. dofleini* in having five intercostal spaces between adpressed toes and in having a different color pattern. Both are robust species having no close relationships to other species of *Bolitoglossa* in northern Central America.

The specimen from Chinajá was found in water in the axil of a large elephant-ear plant (*Xanthosoma*) by day in March. Its stomach contained fragments of beetles and a large roach. The natives did not know salamanders and had no name for them.

Bolitoglossa moreleti mulleri (Brocchi)

Chinajá, 2; Río San Román, 1.

One specimen is a female having a snout-vent length of 80 mm., a tail length of 82 mm., and a total length of 162 mm. It contains 63 large eggs, the largest of which has a diameter of about three millimeters. This specimen has 13 costal grooves, four intercostal spaces between adpressed toes, and 12-13 vomerine teeth. A juvenile having a snout-vent length of 39 mm. and a tail length of 33 mm. has 12 costal grooves, three intercostal spaces between adpressed toes, and 8-8 vomerine teeth. In life these salamanders were uniformly dull brownish black above with a dull creamy yellow irregular dorsal stripe beginning on the occiput and continuing onto the tail. There are no yellow or orange streaks or flecks on the head or limbs. The specimen from the Río San Román was taken from the stomach of a *Pliocercus euryzonus aequalis* and has not been studied in detail, because of its poor condition.

The present specimens show no tendency for the development of a broad irregular dorsal band that encloses black spots or forms irregular dorsolateral stripes, as is characteristic of *B. moreleti mexicanus,* a subspecies that has been reported from La Libertad (Stuart, 1935:35) and Piedras Negras (Taylor and Smith, 1945:545) in El Petén, and from Xunantunich, British Honduras (Neill and Allen, 1959:20).

Schmidt (1936:151) and Stuart (1943:13) found *B. moreleti mulleri* in bromeliads at Finca Samac, Alta Verapaz. Taylor and Smith's (1945:545) and Neill and Allen's (1959:20) specimens of *B. moreleti mexicanus* were obtained from bromeliads, but Neill and Allen (*loc. cit.*) stated that the natives in British Honduras

said that they had found salamanders beneath rubbish on the forest floor. My specimens were obtained from beneath logs on the forest floor in the rainy season. Possibly in drier environments the species characteristically inhabits bromeliads, at least in the dry season.

Bufo marinus (Linnaeus)

Chinajá, 3; 10 km. NNW of Chinajá, 1; 11 km. NNW of Chinajá, 1.

During both visits to Chinajá this large toad was breeding in a small permanent pond in the camp. During the day the toads took refuge in crevices beneath the buildings or beneath large boulders by the pond. At dusk from four to ten males congregated at the pond and called. Tadpoles of this species were in the pond in March and in July. One juvenile was found beneath a rock in the forest, and another was on the forest floor by day.

The natives' name for this species and the following one is *sapo*.

Bufo valliceps valliceps Wiegmann

Chinajá, 52; Río San Román, 8; Sayaxché, 2; Toocog, 1.

This is one of the most abundant, or at least conspicuous, amphibians inhabiting the forest. Breeding congregations were found on February 24, March 2, March 11, and June 27. At these times the toads were congregated at temporary ponds in the forest or along small sluggish streams. Throughout the duration of both visits to Chinajá individual males called almost nightly at the permanent pond at the camp.

The variation in snout-vent length of 20 males selected at random is 56.7 to 72.5 mm. (average, 64.8 mm.). Two adult females have snout-vent lengths of 80.4 and 87.6 mm. In all specimens the parotid glands are somewhat elongated and not rounded as in *Bufo valliceps wilsoni* (see Baylor and Stuart, 1961: 199). My observations on the condition of the cranial crests of the toads in El Petén agree with the findings of Baylor and Stuart (*op. cit.*:198) in that hypertrophied crests are usual in large females. In the shape of the parotids and nature of the cranial crests the specimens from El Petén are like those from the Isthmus of Tehuantepec in México. As I pointed out (1960:53), the validity of the subspecies *Bufo valliceps macrocristatus*, described from northern Chiapas by Firschein and Smith (1957:219) and supposedly characterized by hypertrophied cranial crests, is highly doubtful.

In the toads from El Petén the greatest variation is in coloration. The dorsal ground-color varies from orange and rusty tan to brown, yellowish tan, and pale gray. In some individuals the

flanks and dorsum are one continuous color, whereas in others a distinct dorsolateral pale colored band separates the dorsal color from dark brown flanks. In some individuals the venter is uniform cream color, in others it bears a few scattered black spots, and in still others there are many spots, some of which are fused to form a black blotch on the chest. In breeding males the vocal sac is orange tan. All specimens have a coppery red iris.

Aside from the breeding congregations, active toads were found on the forest floor at night; a few were there by day. Some individuals were beneath logs during the day.

Eleutherodactylus rostralis (Werner)

Chinajá, 10.

Because of the multiplicity of names and the variation in coloration, the small terrestrial *Eleutherodactylus* in southern México and northern Central America are in a state of taxonomic confusion. Stuart (1934:7, 1935:37, and 1958:17) referred specimens from El Petén to *Eleutherodactylus rhodopis* (Cope). Stuart (1941b:197) described *Eleutherodactylus anzuetoi* from Alta Verapaz and El Quiché, Guatemala, suggested that the new species was an upland relative of *Eleutherodactylus rostralis* (Werner), and used that name for the frogs that he earlier had referred to *Eleutherodactylus rhodopis*. Dunn and Emlen (1932:24) placed *E. rostralis* in the synonymy of *E. gollmeri* (Peters). Examination of series of these frogs from southern México, Guatemala, and Costa Rica causes me to think that there are four species; these can be distinguished as follows:

E. rhodopis.—No web between toes; one tarsal tubercle; tibiotarsal articulation reaches to nostril; iris bronze in life.

E. anzuetoi.—No web between toes; a row of tarsal tubercles; tibiotarsal articulation reaches to tip of snout; color of iris unknown.

E. rostralis.—A vestige of web between toes; no tarsal tubercles; tibiotarsal articulation reaches snout or slightly beyond; iris coppery red in life.

E. gollmeri.—A vestige of web between toes; no tarsal tubercles; tibiotarsal articulation reaches well beyond snout; iris coppery red in life.

The presence of webbing between the toes, the absence of tarsal tubercles, and the coppery red iris distinguish *E. rostralis* and *E. gollmeri* from the other species. Probably *E. rostralis* and *E. gollmeri* are conspecific, but additional specimens are needed from Nicaragua and Honduras to prove conspecificity. On the other hand, the characters of the frogs from Chinajá clearly show that they are related to *E. gollmeri* to the south and not to *E. rhodopis* to the north in México.

At Chinajá, *Eleutherodactylus rostralis* was more abundant than

the few specimens indicate, for upon being approached the frogs moved quickly and erratically, soon disappearing in the leaf litter on the forest floor. Most of the specimens were seen actively moving on the forest floor in the daytime; one was found beneath a rock, and one was on the forest floor at night.

Eleutherodactylus rugulosus rugulosus (Cope)

Chinajá, 2; 15 km. NW of Chinajá, 4.

These frogs were found on the forest floor by day. With the exception of one female having a snout-vent length of 69.5 mm., all are juveniles. The apparent rarity of this species at Chinajá may be due to the absence of rocky streams, a favorite habitat of this frog. The local name for this frog is *sapito*, meaning little toad.

Leptodactylus labialis (Cope)

Toocog, 1.

One juvenile having a snout-vent length of 16.4 mm. was found at night beside a pond in the forest. The scarcity of the species of *Leptodactylus* in the southern part of El Petén probably is due to the lack of permanent marshy ponds.

Leptodactylus melanonotus (Hallowell)

Sayaxché, 1.

One individual was found beneath a rock beside a stream in the forest. The local name is *ranita*, meaning little frog.

Syrrhophus leprus Cope

Chinajá, 2; 15 km NW of Chinajá, 1.

An adult female having a snout-vent length of 27.5 mm. was found on the forest floor by day. Two juveniles having snout-vent lengths of 15.5 and 19.0 mm. were beneath rocks on the forest floor. The specimens are typical of the species as defined by Duellman (1958:8).

Hyla ebraccata Cope

Toocog, 66.

This small tree frog congregated in large numbers at a forest pond at Toocog. Between June 30 and July 2 we collected specimens and observed the breeding habits of this and other species at the pond. Calling males were distributed around the pond, where they called from low herbaceous vegetation at the edge of the pond or from plants rising above the water. Calling commenced at dusk

and continued at least into the early hours of the morning. On one occasion a female was observed at a distance of about 50 centimeters away from a calling male sitting on a blade of grass. The female climbed another blade of grass until she was about eight centimeters away from the male, at which time he saw her, stopped calling, jumped to the blade of grass on which she was sitting and clasped her. Clasping pairs were observed on blades of grass and leaves of plants above the water; most pairs were less than 50 centimeters above the surface of the pond.

The eggs are deposited on the dorsal surfaces of leaves above the water. All eggs are in one plane (a single layer) on the leaf. External membranes are barely visible, as the eggs consist of a single coherent mass. Eggs in the yolk plug stage have diameters of 1.2 to 1.4 mm. Seventeen eggs masses were found; these contained from 24 to 76 (average 44) eggs. The jelly is extremely viscous and tacky to the touch. At time of hatching the jelly becomes less viscous; the tadpoles wriggle until they reach the edge of the leaf and drop into the water.

Eleven tadpoles were preserved as they hatched; these have total lengths of 4.5 to 5.0 (average 4.77) mm. Hatchling tadpoles are active swimmers and have only a small amount of yolk. The largest tadpoles preserved have total lengths of 13.0 and 13.5 mm. At this size distinctive sword-tail and bright coloration have developed.

Description of fully developed tadpole (KU 59986): Total length, 13.5 mm.; tail-length, 8.4 mm., 62 per cent of total length. Snout, in dorsal view, bluntly rounded; in lateral view less bluntly rounded; body depressed; head flattened; mouth terminal; eye large, its diameter 25 per cent of length of body; nostrils near tip of snout and directed anteriorly; spiracle sinistral and situated posteroventrad to eye; cloaca median. Tail-fin thrice depth of tail-musculature, which extends beyond posterior end of tail-fin giving sword-tail appearance (Fig. 2). In life, black stripe on each side of body and on top of head; black band on anterior part of tail

Fig. 2. Tadpole of *Hyla ebraccata* (KU 59986) from Toocog, El Petén, Guatemala. × 6.

and another on the posterior part; body and anterior part of tail creamy yellow; dark red band between black bands on tail. Mouth terminal, small, its width about one-fifth width of body; fleshy ridge dorsally and ventrally; row of small papillae on ventral lip; no lateral indentations of lips; upper beak massive, convex, and finely serrate; lower beak small and mostly concealed behind upper; no teeth (Fig. 3).

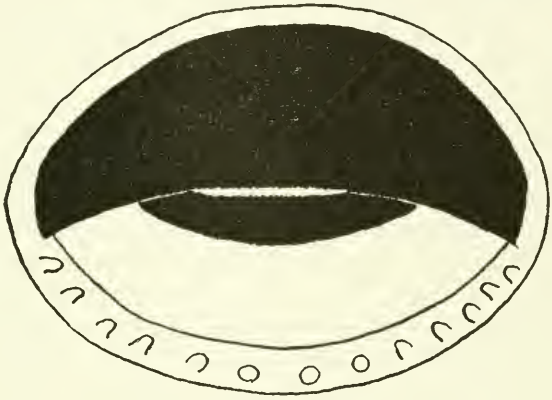


Fig. 3. Mouthparts of larval *Hyla ebraccata* (KU 59986) from Toocog, El Petén, Guatemala. × 100.

Hyla loquax Gaige and Stuart

Toocog, 14.

These specimens were found at night when they were calling from low vegetation in a forest pond. Most of the frogs were several meters away from the edge of the pond. Although two clasping pairs were found, we obtained no eggs or tadpoles referable to this species.

Hyla microcephala martini Smith

Chinajá, 1; Toocog, 21.

The specimen from Chinajá was calling from a small bush at the edge of a temporary grassy pond in a clearing in the forest. At Toocog this species was closely associated with *Hyla ebraccata;* males were calling from herbaceous vegetation in and around the forest pond. These frogs were not so abundant in the forest at Toocog as they were around ponds on the savanna at La Libertad.

Hyla picta (Günther)

Toocog, 8.

This small tree frog was calling from herbs in a pond in the forest on June 30 and July 2. The voice is weak; probably greater numbers of males were present than are indicated by the few specimens collected, for the din from the more vociferous species made it impossible to hear *Hyla picta* unless one was calling close by.

Hyla staufferi Cope

Chinajá, 1.

This individual was calling from a low bush in the clearing at Chinajá. None was found in the pond in the forest at Toocog. Stuart (1935:38) and Duellman (1960:63) noted that *Hyla staufferi* breeds early in the rainy season. Nevertheless, I think early breeding habits do not account for the near absence of this species in our collections from southern El Petén. In early July, 1960, a few individuals were heard at a pond on the savanna at La Libertad. In mid-July of the same year they were calling sporadically from temporary ponds in the lower Motagua Valley. Possibly the individual collected at Chinajá was accidentally transported there in cargo from Toocog, from which camp at the edge of the savanna planes fly to Chinajá weekly. My observations on this species throughout its range in México and Central America indicate that it inhabits savannas and semi-arid forests and usually is absent from heavy rainforest. Stuart (1948:34) obtained this species at Cubilguitz in the lowlands of Alta Verapaz.

Phyllomedusa callidryas taylori Funkhouser

Toocog, 25.

Between June 30 and July 2 this species was abundant at a pond in the forest at Toocog. Calling males were as high as five meters in bushes and trees around the pond. At dusk males were observed descending a vine-covered tree at the edge of the pond; this strongly suggests that the frogs retreat to this tree and others like it for diurnal seclusion. Clasping pairs were found on branches and leaves above the water. The eggs are deposited in clumps usually on vertical leaves, but sometimes on horizontal leaves or on branches, vines, and aerial roots above the water. Twenty-six clutches of eggs contained from 14 to 44 (average 29) eggs. In a clutch in which the eggs are in yolk plug stage the average diameter of the embryos is 2.3 mm. and that of the vitelline

membranes, 3.4 mm. Most of the eggs are in the external part of the gelatinous mass; the jelly is clear. The yolk is pale green, and the animal pole is brown. As development ensues, the yolk becomes yellow and the embryo first dark brown and then pale grayish tan. Upon hatching the tadpoles wriggle free of the jelly and drop into the water. One clutch of 19 eggs was observed to hatch in three minutes. Apparently, on dropping into the water the hatchling tadpoles go to the bottom of the pond, for one or two minutes pass from the time they enter the water until they reappear near the surface. The average total length of seven hatchling tadpoles is 7.4 mm. There is a moderate amount of yolk, but this does not form a large ventral bulge. Large tadpoles congregate in the sunny parts of the pond, where they were observed just beneath the surface. Many had their mouths at the surface. Except for constant fluttering of the tip of the tail, they lie quietly with the axis of the body at an angle of about 45 degrees with the surface of the water.

Description of tadpole (KU 60006): total length, 24.5 mm.; tail-length, 15.4 mm.; body broader than deep; head moderately flattened; snout viewed from above blunt; nostrils close to snout and directed dorsally; eyes of moderate size and directed laterally; mouth directed anteroventrally; anus median; spiracle ventral, its opening just to left of midline slightly more than one-half distance from tip of snout to vent. Tail-fin slightly more than twice as deep as tail musculature, which curves upward posteriorly; tail-fin narrowly extending to tip of tail (Fig. 4). Color in life pale gray; in preservative white with scattered melanophores; tail-fin transparent.

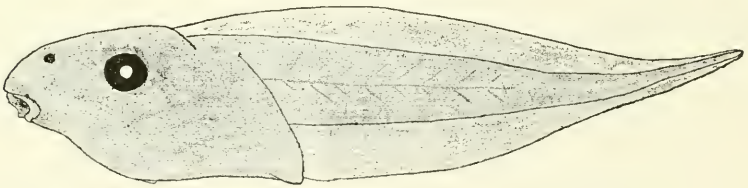


Fig. 4. Tadpole of *Phyllomedusa callidryas taylori* (KU 60006) from Toocog, El Petén, Guatemala. × 4.

Upper lip having single row of papillae laterally, but none medially; lower lip having single row of papillae; no lateral indentation of lips; two or more rows of papillae at lateral corners of lips; tooth-rows 2/3; second upper tooth row as long as first, interrupted medially; inner lower tooth-row as long as upper rows,

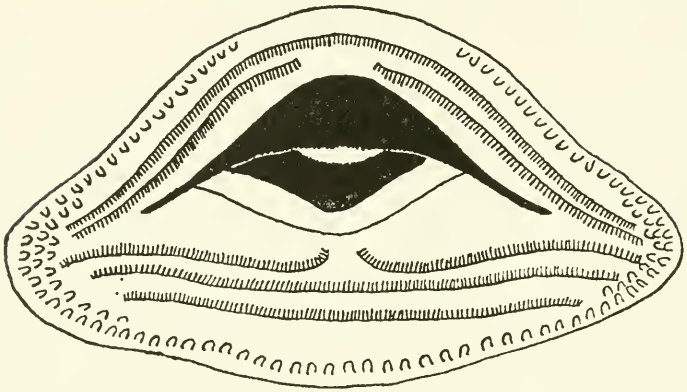


FIG. 5. Mouthparts of larval *Phyllomedusa callidryas taylori* (KU 60006) from Toocog, El Petén, Guatemala. × 30.

interrupted medially; second and third lower rows decreasingly shorter; upper beak moderate in size and having long lateral projections; lower beak moderate in size; both beaks finely serrate (Fig. 5).

Smilisca baudini (Duméril and Bibron)

Chinajá, 9; 20 km. NNW of Chinajá, 42; Río de la Pasión, 1; Río San Román, 5; Sayaxché; Toocog, 2.

Individuals of this species were found at night sitting on bushes and small trees in the forest in February and March and again in June and July. One was in the axil of a leaf of a *Xanthosoma.* In June and July males were heard nearly every night. The series of specimens from 20 kilometers north-northwest of Chinajá was taken from a breeding congregation in a shallow muddy pool in the forest. Tadpoles of this species were in small, often muddy pools in the forest. To my knowledge *Smilisca baudini* is the only hylid to breed in these pools at Chinajá, although perhaps *Smilisca phaeota* also utilizes them. The only other amphibian at Chinajá known to breed in the pools is *Bufo valliceps valliceps.* Although two specimens were on bushes at night at Toocog, *Smilisca baudini* was not present at the pond where five other species of hylids were breeding. Nevertheless, *Smilisca baudini* was calling from two ponds on the savannas near La Libertad. All of the specimens from southern El Petén have yellow or yellowish white flanks and ventrolateral surfaces.

Smilisca phaeota cyanosticta (Smith)

Chinajá, 4; 10 km. NNW of Chinajá, 1.

All specimens were found in February and March. Those from Chinajá were obtained from *Xanthosoma* and bromeliads; the individual from 10 kilometers north-northwest of Chinajá is an adult male that was calling from a puddle in a fallen tree on March 13. A juvenile having a snout-vent length of 34.7 mm. lacks the pale blue spots on the thighs; instead, the anterior and posterior surfaces of the thighs are bright red.

Hypopachus cuneus nigroreticulatus Taylor

Toocog, 1.

An adult male having a snout-vent length of 41.7 mm. was found at night on the forest floor at the edge of a temporary pond. In life the dorsum was dark brown with chocolate brown markings; the stripe on the side of the head was white; the middorsal stripe was pale orange; the belly was black and white, and the iris was a bronze color.

Characteristically this species inhabits savannas and open forest; thus, its occurrence in the rainforest at Toocog is surprising. This is the southernmost record for the species in El Petén; to the south in the highlands it is replaced by the smaller *Hypopachus inguinalis*, having rounded, instead of compressed, metatarsal tubercles.

Rana palmipes Spix

Chinajá, 11; 15 km. NW of Chinajá, 1; 20 km. NNW of Chinajá, 1.

With the exception of one recently metamorphosed juvenile having a snout-vent length of 30.7 mm. that was found on the forest floor by day on June 24, and one that was found beside a pool in a cave, all individuals were found at temporary woodland pools or along sluggish streams at night. The largest specimen is a female having a snout-vent length of 107 mm.

Rana pipiens Schreber

Chinajá, 1; 20 km. NNW of Chinajá, 1; Río San Román, 1; Toocog, 1.

All specimens were found near water at night. The largest individual is a female having a snout-vent length of 112.5 mm.

Crocodylus moreleti Duméril and Duméril

Chinajá, 1; Río San Román, 1.

One specimen was obtained from a quiet pool in the Río San

Román at night; another was found in a small sluggish stream at Chinajá. Two large individuals were seen in tributaries to the Río San Román. On the savannas at Toocog two small individuals were obtained in the dry season, at which time the crocodiles apparently were migrating to water. The local name for this species is *lagarto.*

Chelydra rossignoni (Bocourt)

Chinajá, 1; 20 km. NNW of Chinajá, 1.

The paucity of specimens of *Chelydra* from Central America has resulted in rather inadequate diagnoses of various populations. The present specimens have carapace lengths of 250 and 238 mm. and plastral lengths of 185 and 176 mm. The length of carapace/bridge ratio is 6.0 and 6.1 per cent. Each individual has four barbels, the median pair of which are extremely long. In KU 55977 the lateral pair of barbels is forked at the base. The relative length of the plastral bridge in these specimens compares favorable with the ratio (.06-.08) given by Schmidt (1946:4) for five specimens from Honduras. *Chelydra serpentina,* which may occur sympatrically with *C. rossignoni* in some parts of Central America, has a narrower plastral bridge and only two barbels beneath the chin. Futhermore, *C. rossignoni* and *C. osceola* in Florida have long, flat tubercles on the dorsal and lateral surfaces of the neck, whereas *C. serpentina* has short, round tubercles.

The specimen from Chinajá was found in a small sluggish stream; the other individual was in a muddy pool in the forest. The local name is *sambodanga.*

Claudius angustatus Cope

20 km. NNW of Chinajá, 1.

One specimen was unearthed from the bank of a small muddy stream by a bulldozer. This individual represents the second record for the species in Guatemala; the first was provided by specimens, likewise found in muddy waters, at Tikal (Stuart, 1958:19). The local name is *caiman.*

Kinosternon acutum Gray

20 km. NNW of Chinajá, 4; 30 km. NNW of Chinajá, 2.

These turtles were found on the forest floor, in small sluggish streams, and in pools in the forest. One adult male had, in life, the top of the head yellow with black spots; the stripes on the head and neck were red. Specimens were obtained both in the dry

and rainy seasons. The local name for both species of *Kinosternon* is *pochitoque*.

Kinosternon leucostomum Duméril and Bibron

Chinajá, 3; 15 km. NW of Chinajá, 1; 20 km. NNW of Chinajá, 2.

Individuals of this turtle were found on the forest floor and in small sluggish streams. In life most specimens had a tan or pale brown head with pinkish tan stripes on the head and neck. All individuals were obtained in Febuary and March. No ecological differences between this species and *K. acutum* were evident.

Staurotypus triporcatus (Wiegmann)

Paso Subín, 1.

This species is represented in the collection by one complete shell found on the bank of the Río Subín. The carapace has a length of 292 mm. The local name is *Guao*. Natives stated that this turtle was not uncommon in clear rivers and lakes, a habitat suggested for the species by Stuart (1958:19).

Dermatemys mawi Gray

Chinajá, 1; Río San Román, 4.

The record from Chinajá is based on a carapace found in a chiclero camp, where the turtle evidently had been brought for food. The four specimens from the Río San Román were obtained from edges of deep pools in clear water. In adult males the top of the head was reddish orange in life. One of the specimens from the Río San Román currently is living in the Philadelphia Zoological Gardens. The local name for this turtle is *tortuga blanca*; it is sought for its meat.

Geoemyda areolata (Duméril and Bibron)

Chinajá, 2.

Two specimens were obtained from dense forest at Chinajá. The local name is *mojina*.

Pseudemys scripta ornata (Gray)

Paso Subín, 1.

One subadult was obtained from clear water in the Río Subín. The stripes on the head and neck were yellow; there was no red "ear" on the side of the head. The stripes on the forelimbs were orange, and the ocelli on the carapace were red. The local name is *jicotea*.

Coleonyx elegans elegans Gray

Toocog, 1.

One adult male having a snout-vent length of 89 mm. was found beneath a log in the forest. Locally this gecko is known as *escorpión;* the natives believe it to be deadly poisonous. The use of the name *escorpión* seems to be restricted to lizards thought to be venomous. Nearly everywhere in México and Central America some species of lizard carries this appellation. In El Petén I heard the name used only for *Coleonyx elegans* and *Thecadactylus rapicaudus*; in the lowlands of Guerrero, México, the name is applied to geckos of the genus *Phyllodactylus.* The venomous lizards of the genus *Heloderma* in the lowlands of western México are called *escorpiónes.* In the mountains of southern México various skinks of the genus *Eumeces,* as well as lizards of the genus *Xenosaurus,* carry the same appellation. *Abronia* in the mountains of México and *Gerrhonontus* throughout México and Central America likewise are called *escorpiónes.* Although many people in various parts of Middle America consider most lizards poisonous, there is a unanimity of opinion concerning the venomous qualities of the various kinds of *escorpiónes.* I know of only two other lizards in Middle America that are so uniformly regarded in native beliefs; these are *Enyaliosaurus clarki* in the Tepalcatepec Valley in Michoacán, called *nopiche,* and *Phrynosoma asio* in western México, called *cameleón.*

Sphaerodactylus lineolatus Lichtenstein

15 km. NW of Chinajá, 1; Toocog, 1.

These small geckos were much more abundant than the few specimens indicate. They frequently were seen on the trunks of corozo palms, where they quickly took refuge in crevices at the bases of the fronds. The specimen obtained at Toocog was under the bark of a standing dead tree. In life the ventral surface of the tail was orange. The individual from Chinajá was in the leaf litter on the ground at the base of a dead tree.

Thecadactylus rapicaudus (Houttuyn)

15 km. NW of Chinajá, 1; 20 km. NNW of Chinajá, 2.

Two specimens were found beneath the bark of standing dead trees; another was found in the crack in the trunk of a mahogany tree about 13 meters above the ground. In life the dorsum was

yellowish tan with dark brown markings; the venter was yellowish tan with brown flecks, and the iris was olive-tan. The largest specimen is a male having a snout-vent length of 95 mm.; all specimens have regenerated tails. Individuals when caught twisted their bodies and attempted to bite; upon grabbing a finger they held on with great tenacity.

Anolis biporcatus (Wiegmann)

14 km. NNW of Chinajá, 1; 17 km. NNW of Chinajá, 1; 20 km. NNW of Chinajá, 3; 30 km. NNW of Chinajá, 1; Sayaxché, 1.

All specimens of this large anole were obtained from trees. Some individuals were found in the tops of trees immediately after they were felled. My limited observations on this anole suggest that it is an inhabitant of the upper levels of the forest. In life an adult male from 20 kilometers north-northwest of Chinajá was brilliant green above; the eyelids were bright yellow; the belly was white. The outer part of the dewlap was pale orange, and the median part was pinkish blue. A juvenile having a snout-vent length of 47 mm. and a tail length of 86 mm. was pale grayish green with pale gray flecks on the dorsum. The largest male has a snout-vent length of 98 mm. and a tail length of 217 mm.; the same measurements of the largest female are 89 and 213 mm. This species, together with all other anoles, is known locally as *toloque*.

Anolis capito Peters

Chinajá, 2; 14 km. NNW of Chinajá, 1; Río de la Pasión, 1.

All individuals were observed on trunks of trees between heights of three and ten meters above the ground. The largest male has a snout-vent length of 81 mm. and a tail length of 155 mm.; the same measurements of the largest female are 87 and 150 mm. The streaked brown dorsum, combined with the lizards' habit of pressing the body against the trunks of trees, make this anole especially difficult to see.

Anolis humilis uniformis Cope

Chinajá, 24; 15 km. NW of Chinajá, 22; 20 km. NNW of Chinajá, 6; Sayaxché, 1.

This small dull brown anole is a characteristic inhabitant of the forest floor, where the lizards move about in a series of quick, short hops and thus easily evade capture. Three individuals were found on small bushes, and four were on the bases of trees; otherwise, all were observed on the ground. Observations indicate that

this species is active throughout the day, except during and immediately after heavy rains. The males have a deep red dewlap with a dark blue median spot.

Anolis lemurinus bourgeaei Bocourt

Chinajá, 11; 20 km. NNW of Chinajá, 4; 30 km. NNW of Chinajá, 2; Río de la Pasión, 1; Río San Román, 1; Sayaxché, 8; Toocog, 6.

This moderate-sized anole characteristically inhabits the low bushes and bases of trees in the forest. Individuals were most readily observed on the buttresses of some of the gigantic mahogany and ceiba trees. When approached the lizards usually ran around the tree or ducked to the other side of the buttress; if the observer moved closer, they jumped to the ground and ran off. None was observed to ascend large trees. Some individuals were observed foraging on the forest floor; these took shelter on the bases of trees. One individual was sleeping on a palm frond at night. The adult males have a uniformly orange-red dewlap.

Anolis limifrons rodriguezi Bocourt

15 km. NW of Chinajá, 2; 20 km. NNW of Chinajá, 1.

In dry forests and more open situations than occur at Chinajá this little anole is abundant, but in the wet forests of southern El Petén, only three specimens were found. Two were on palm fronds about two meters above the ground; the other was on a low bush. I suspect that ecologically this species overlaps *A. humilis uniformis* and *A. lemurinus bourgeaei,* but too few observations are recorded to justify a definite statement at this time.

Anolis sericeus sericeus Hallowell

Chinajá, 2; Sayaxché, 1; Toocog, 1.

This small anole is common and widespread in the Atlantic lowlands of southern México and northern Central America; usually it inhabits sub-humid regions. Consequently, its presence in the wet forests of southern El Petén was unexpected. The specimens from Chinajá were sleeping on low bushes at night, whereas the others were found on bushes by day.

Basiliscus vittatus Wiegmann

Chinajá, 6; Río de la Pasión, 1; Río San Román, 1; Sayaxché, 3; Toocog, 1.

Individuals of this abundant species were most frequently seen in dense bushes along the margins of rivers or small streams. None was observed far from water. These lizards, like the anoles, are known locally as *toloque.*

Corythophanes cristatus (Merrem)

Chinajá, 3; 20 km. NNW of Chinajá, 1.

Three individuals were found on tree trunks; the fourth was on a thick vine about one meter above the ground. The two largest males have snout-vent lengths of 121 and 115 mm. and tail lengths of 265 and 243 mm. The largest female (KU 59603), obtained on June 28, has a snout-vent length of 125 mm. and a tail length of 247 mm. This individual contained eight ova varying in greatest diameter from 10.6 to 12.2 (average 11.1) mm. Also present are numerous ovarian eggs having diameters up to about 3.5 mm.

One of the large males displayed a defensive behavior prior to capture. When first observed the lizard was clinging to a tree trunk about one and one-half meters above the ground. When I approached, the lizard turned its flanks towards me; then it flattened the body laterally, extended the dewlap, opened its mouth, and made short rushing motions. When touched it bit viciously. On the ground these lizards have a rather awkward bipedal gait that is much slower than in *Basiliscus vittatus*.

In life an adult male (KU 55804) was reddish brown dorsally with dark chocolate brown markings; the venter was creamy white, and the iris was dark red. The natives call this lizard *piende jente*.

Iguana iguana rhinolopha Wiegmann

Río San Román, 2.

The *iguana*, as this lizard is called locally, seems to be uncommon in the forested areas of southern El Petén. Possibly this is due to the fact that the flesh of this lizard is relished as food by the natives. My two specimens were in large trees at the edge of the river.

Laemanctus deborrei Boulenger

Chinajá, 1; Toocog, 5.

On June 26 a female having a snout-vent length of 129 mm. and a tail length of 502 mm. was found on a bush in the forest. The lizard, when approached, faced the collector and opened its mouth. In life the dorsum was bright green; the lateral stripe was white, and the iris was yellowish brown. This specimen contained four ova having lengths of 13.4 to 14.2 (average 13.9) mm.

On June 30 at Toocog five white-shelled eggs were found in a rotting log. Measurements of the eggs are—length, 23.5 to 25.0 (average 24.2) mm.; width, 15.0 to 15.5 (average 15.4) mm. These eggs hatched on August 30. The five young had snout-vent lengths

of 43 to 45 (average 44) mm., and tail lengths of 137 to 140 (average 138) mm. In life the hatchlings had a dull dark green dorsum, pale bright green venter and stripes on head, and reddish brown iris. In preservative the hatchlings are creamy tan above with five or six square dark brown blotches middorsally.

The natives consider this lizard to be one of the anoles; consequently, it is known as *toloque*.

Lepidophyma flavimaculatum flavimaculatum Duméril

Chinajá, 8; 15 km. NW of Chinajá, 2.

Individuals were found beneath logs on the forest floor or moving about in the litter on the forest floor. One was observed crawling across a trail during a heavy rain. In some adults the tan dorsal spots are large and distinct; in others the spots are small and indistinct. Two juveniles, apparently recent hatchlings, were found on June 28 and July 5. These specimens have snout-vent lengths of 29 mm. and tail lengths of 38 and 41 mm.

Eumeces schwartzei Fischer

Chinajá, 1.

One specimen (KU 59551) was found on the forest floor at midday; it is an adult female having a snout-vent length of 125 mm. and a tail length of 210 mm. This specimen is larger than those recorded by Taylor (1936:99) and extends the known range of the species south of Ramate, approximately 125 kilometers south-southwestward to Chinajá.

Eumeces sumichrasti (Cope)

20 km. NNW of Chinajá, 1.

One adult male having a snout-vent length of 82 mm. was found beneath a palm frond on the forest floor. In life the dorsum was dull brown; the chin was cream; the belly was yellow, and the underside of the tail was orange. A juvenile having a black body, yellow dorsal stripes, and a bright blue tail was observed on the forest floor.

Scincella cherriei cherriei (Cope)

Chinajá, 2; 30 km. NNW of Chinajá, 1; Toocog, 1.

All individuals of this lizard were found in the leaf litter on the forest floor; many escaped capture. In life the tail is dull bluish gray. The number of dorsal scales varies from 59 to 61 (average

60); thus, these specimens fall within the range of variation of S. *cherriei cherriei,* and thereby differ from S. *cherriei stuarti* to the west and S. *cherriei ixbaac* to the north.

Ameiva festiva edwardsi Bocourt

Chinajá, 16; 15 km. NW of Chinajá, 10; Sayaché, 4; Toocog, 1.

This abundant terrestrial lizard, locally called *lagartijo,* is found throughout the forest. A juvenile obtained on March 14 at Sayaxché has a snout-vent length of 42 mm. and a prominent umbilical scar. Other juveniles were observed at Chinajá in February and March, thereby indicating that the young probably hatch in the early part of the year. Juveniles have bright blue tails.

Celestus rozellae Smith

20 km. NNW of Chinajá, 2.

Two specimens were obtained from trees by workmen in February. These lizards have snout-vent lengths of 70 and 83 mm. and tail lengths of 133 and 135 mm. There are 21 and 23 lamellae beneath the fourth toe; each has 31 longitudinal rows of scales around the body.

Boa constrictor imperator Daudin

15 km. NW of Chinajá, 1; 20 km. NNW of Chinajá, 2; Toocog, 1.

All specimens were found on the forest floor. One individual was found in combat with a large *Drymarchon corais melanurus.* Apparently, the *Drymarchon* was attempting to devour the *Boa,* which had a total length of 1683 mm. Locally this snake is called *masacuata;* it is one of the few snakes believed by the local inhabitants to be non-poisonous.

Clelia clelia clelia Daudin

15 km. NW of Chinajá, 1; 20 km. NNW of Chinajá, 1.

One specimen is represented only by the head; the snake was killed on the forest floor by workmen. Another individual was found in a pool of water at the base of a limestone outcropping in the forest; this specimen (KU 58167) is a female having a body length of 2220 mm. and a total length of 2634 mm. This snake contained 22 ova averaging 56 x 23 mm. Both specimens were uniform shiny black above and cream-color below. The local name is *sumbadora.*

Coniophanes bipunctatus bipunctatus (Günther)

Chinajá, 1.

This snake was found on the forest floor by day; it is a male having 130 ventrals, an incomplete tail; cream-colored belly, and a pair of large brown spots on each ventral scute.

Coniophanes fissidens fissidens (Günther)

Toocog, 1.

This male specimen was found beneath a rock in a sink hole. It has 122 ventrals and 77 caudals. A narrow temporal stripe extends along the upper edge of the anterior temporal and the lower edge of the upper secondary temporal. The belly is ashy white with a pair of small black spots on each ventral.

Coniophanes imperialis clavatus (Peters)

Chinajá, 3.

All specimens were found on the forest floor by day. These small snakes are capable of rapid movement and quickly disappear in the litter on the ground. Two individuals evaded capture. The belly is creamy white anteriorly and vermillion red posteriorly.

Dryadophis melanolomus laevis (Fischer)

Chinajá, 3.

These snakes, locally known as *sumbadora,* were found on the forest floor; two others were seen, but escaped. The variation in coloration has been a source of confusion in this species in northern Central America (see Stuart, 1941:86). All of the present specimens are males: KU 55709 has 178 ventrals, 121 caudals, and a total length of 914 mm.; the dorsum is olive-tan with six darker cross-bars on the neck; the belly is creamy white. KU 58160 has 188 ventrals, 123 caudals, and a total length of 1365 mm.; the dorsum is uniform olive-brown, except that some dorsal scales at midbody have black anterior borders like *D. melanolomus melanolomus* has in the Yucatan Peninsula; the venter is pale yellow. KU 58158 has 179 ventrals, 122 caudals, and a total length of 723 mm.; the dorsum is rich chocolate brown with eight dark cross-bars on the neck; the belly is bright orange.

Stuart (1941a:87) stated that in life two distinct color phases were observed in specimens collected by him in Alta Verapaz, Guatemala. One had an olive-brown dorsum and the other, a

reddish orange dorsum. Stuart made no mention of variation in the color of the venter. Similar variation is known in *D. melanolomus alternatus* in Costa Rica, where some individuals have orange-red venters. This color phase has been recognized as a distinct species, *Dryadophis sanguiventris,* by Taylor (1954:722). Examination of 18 specimens from Costa Rica shows no differences in scutellation, nor geographic segregation of two populations. I am convinced that the red-bellied *Dryadophis* in Costa Rica, like those in Guatemala, represent a color phase of the subspecies inhabiting those areas and that *Dryadophis sanguiventris* Taylor is a synonym of *Dryadophis melanolomus alternatus* (Bocourt).

Drymarchon corais melanurus (Duméril, Bibron and Duméril)

15 km. NW of Chinajá, 1; Sayaxché, 1.

The specimen from Sayaxché was found at the edge of a clearing in the forest; that from 15 kilometers northwest of Chinajá was found on the forest floor coiled with a *Boa constrictor imperator,* which the *Drymarchon* apparently was trying to eat. The *Drymarchon* is a giant specimen having a total length of 2950 mm. (see Duellman, 1961;368). The *Boa* with which it was coiled has a total length of 1683 mm. I was attracted to the snakes by a loud thrashing noise. When I approached the writhing mass, the snakes separated, but I was able to see that the *Drymarchon* had its teeth firmly imbedded in the posterior part of the head of the *Boa.* From the *Drymarchon* I forced the regurgitation of a recently ingested *Bothrops nummifer nummifer* having a total length of 953 mm. These observations show that the snake-eating capabilities of *Drymarchon* can hardly be over-estimated.

In both *Drymarchon* the anterior one-half of the body is olive-tan, which changes to bluish black posteriorly. The local name is *sumbadora.*

Drymobius margaritiferus margaritiferus (Schlegel)

Chinajá, 3; Sayaxché, 1.

All individuals were obtained in clearings in the forest by day in the rainy season. Two individuals each contained a *Similisca baudini* and another contained a *Bufo valliceps valliceps.* Locally this snake is known by the appropriate name of *ranera.*

Imantodes cenchoa leucomelas Cope

Chinajá, 4.

With the exception of one that was found dead in camp, all

individuals were taken from low vegetation by day. The dorsum is creamy tan with 28 to 35 (average 32) chocolate brown blotches, and the venter is ashy white with small brown flecks. Three males have 238 to 248 (average 244) ventrals and 148 to 154 (average 151) caudals; one female has 239 ventrals and 142 caudals. The largest specimen, a male, has a body length of 660 mm. and a total length of 943 mm.

Lampropeltis doliata polyzona Cope

Chinajá, 1.

One female (KU 57156) having 230 ventrals and 54 caudals was found on the forest floor by day. This individual has a black snout with a white bar across the nasals and prefrontals, a white spot in the middle of the frontal, and a white band across the temporals and parietals that is bordered posteriorly by a black band. There are 28 white and 28 red rings on the body. The tips of the red scales are darkened. The black rings between the white and red rings are not so expanded as to interrupt the white rings dorsally as in *L. doliata abnorma* as identified by Stuart (1948:70). Locally this snake, like all red, black, and white or yellow banded snakes, is called *coral* or *coralillo.*

Leptodeira frenata malleisi Dunn and Stuart

Toocog, 1.

This specimen, a male having 173 ventrals and 69 caudals, was found beneath the bark on a log in the forest. In life the dorsum was pinkish tan with 36 chocolate brown blotches on the body; the venter was rosy pink.

Leptodeira septentrionalis polysticta Günther

Chinajá, 3; Toocog, 11.

If numbers of specimens are indicative of abundance, this is the most common snake in southern El Petén. All were found at night in the rainy season. At a pond in the forest at Toocog these snakes were observed on low vegetation, on the ground, and in the water. Evidently they congregate at breeding choruses of frogs. One *Leptodeira* contained a *Smilisca baudini* and another contained eggs of *Phyllomedusa callidryas taylori.* The natives call this snake *nahuyaca.*

Leptophis ahaetulla praestans (Cope)

13 km. NNW of Chinajá, 1; 20 km. NNW of Chinajá, 1.

Both specimens were obtained from trees when they were felled. One individual (KU 55716) has a body length of 1345 mm. and a total length of 2035 mm. In life the entire snake was uniform bright green; the eye was yellow. In preservative the dorsum is dark blue, and the venter is green.

Leptophis mexicanus mexicanus Duméril, Bibron and Duméril

Chinajá, 1; 15 km. NW of Chinajá, 1; Sayaxché, 4.

All specimens came from low trees in the forest. The largest specimen is a male having a body length of 724 mm. and a total length of 1236 mm. In life the middorsum was a golden tan; the top of the head was a vivid green. One individual had ingested a *Smilisca baudini*. The local name is *bejuquillo*.

Ninia sebae sebae (Duméril, Bibron and Duméril)

Toocog, 1.

This specimen, a male having 144 ventrals and 55 caudals, was found beneath bark on a log in the forest. There is a black band five scales in length on the nape followed posteriorly by a red band six scales in length and then by a complete black band one and one-half scales in length. The rest of the body is dull red with 16 incomplete black bands one to one and one-half scales in length on the anterior two-thirds of the body.

Oxybelis aeneus aeneus (Wagler)

Chinajá, 1; 20 km. NNW of Chinajá, 1.

One individual was found in a low tree; the other was in a bush. Both specimens are males; the largest has a body length of 754 mm. and a total length of 1286 mm. Bogert and Oliver (1945:388) distinguished *O. aeneus aeneus* in Central and South America from *O. aeneus auratus* in México in that the diameter of the eye is more than the length of the internasal, whereas in *O. aeneus auratus* the diameter of the eye is less than the length of the internasal. Stuart (1958:27) stated that on the basis of this character three specimens from Tikal in northeastern El Petén definitely were *O. aeneus aeneus*. Of the present specimens from southern El Petén, one has an internasal:eye ratio of 1.08; the other has a ratio of 0.87. A careful review of these snakes is needed to verify the validity of the characters used to separate the subspecies

and to determine areas of intergradation. The local name for the vine-snake is *bejuquillo*.

Pliocercus euryzonus aequalis Salvin

Chinajá, 1; Río San Román, 1.

These specimens are tentatively referred to *P. euryzonus*. KU 57160 is a female having 130 ventrals, 87 caudals, and 23 black rings on the body; KU 58150 is a juvenile having 128 ventrals, 79 caudals, and 27 black rings on the body. In both specimens the tip of the snout is yellow; a broad yellow band on the parietals and

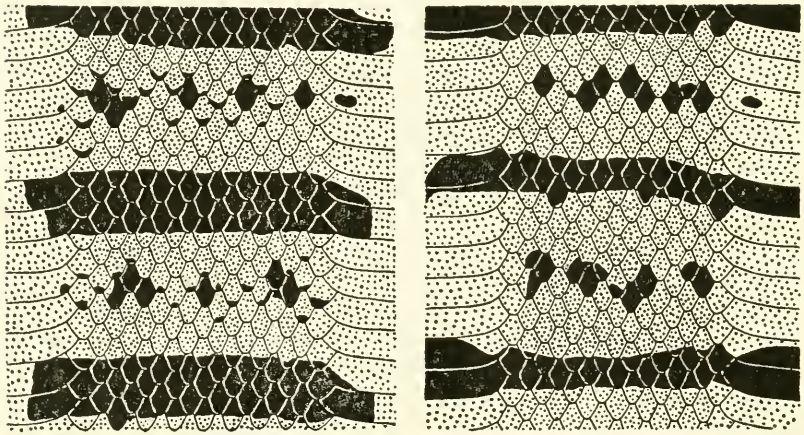


FIG. 6. Dorsal color patterns of *Pliocercus euryzonus aequalis* (A) and *Micrurus affinis apiatus* (B).

temporals is bordered posteriorly by a black band on the nape. The black rings on the body are not bordered by yellow, but black rings on the tail have yellow borders ventrally. In the red interspaces between the black rings, black flecks and spots, especially posteriorly, tend to form secondary black rings (Fig. 6a). According to Stuart (1948:71), *P. euryzonus aequalis* has 25 to 27 black rings on the body, whereas *P. elapoides salvini*, which also occurs in El Petén, has 15 to 23 black rings.

The specimen from the Río San Román contained a partly digested *Bolitoglossa moreleti mulleri*. Locally *Piocercus* is called *coral* or *coralillo*.

Pseustes poecilonotus poecilonotus (Günther)

Chinajá, 3; 20 km. NNW of Chinajá, 1.

Two juveniles were on the forest floor; one juvenile and an adult were on low bushes. The juveniles have a tan dorsum with reddish brown blotches; the belly is gray, and the iris is cream-color above and brown below. The one adult is olive-brown above and creamy white below on the anterior three-fourths of the body; posteriorly it is black above and below. There are no paravertebral dark stripes nor pale spots on the dorsal scales.

Two specimens (one juvenile and the adult) when encountered compressed the anterior part of the body laterally and struck repeatedly. Locally the adults are called *sumbadora.*

Sibon dimidiata dimidiata (Günther)

20 km. NNW of Chinajá, 2.

Both snakes were obtained from trees when they were felled. In life the dorsum was pinkish orange with dark chocolate brown blotches narrowly edged with black.

Sibon nebulata nebulata (Linnaeus)

20 km. NW of Chinajá, 1.

This specimen, a male having a body length of 544 mm. and a tail length of 198 mm., was found in a felled tree. In life the belly was pink and black; the dorsal black blotches were narrowly outlined with pink.

Spilotes pullatus mexicanus (Laurenti)

Chinajá, 3; 20 km. NNW of Chinajá, 1; Sayaxché, 1.

This large snake, locally called *mica,* seems to be equally at home on the ground and in low trees and bushes. It is fast moving for a large snake; two individuals escaped capture. The natives said that this snake eats other snakes, but examination of stomachs revealed no supporting evidence.

Stenorrhina degenhardti (Berthold)

Chinajá, 1.

This specimen, a female having 158 ventrals, 37 caudals, and a total length of 489 mm., was found on the forest floor. On the olive-brown dorsum are 27 irregular, narrow, dark brown, transverse bands. The head is uniform olive-brown; the chin and labials are

cream-color. The venter is cream-color with a row of brown spots forming a midventral stripe. A large spider was found in the stomach.

I have refrained from assigning a subspecific name to this snake. Cursory examination of specimens from throughout México and Central America reveals a bewildering array of variation in coloration that suggests that the subspecies *mexicanus* is not recognizable, or that two species occur sympatrically in parts of southern México and northern Central America.

Tretanorhinus nigroluteus lateralis Bocourt

Chinajá, 1.

A single male having 136 ventrals, 75 caudals, and a total length of 407 mm. was found by a stream in camp. The dorsum is pale grayish tan with 34 pairs of small chocolate brown spots, some of the anterior ones of which are connected across the back. A cream-colored lateral stripe is on the third and fourth dorsal scale-rows anteriorly and the second and third rows posteriorly. The lower dorsal scale rows are black. The venter is dark grayish brown with cream-colored flecks anteriorly and creamy gray posteriorly where the dark color is restricted to the midventral region and the lateral edges of ventrals and first dorsal scale-row.

Xenodon rabdocephalus mexicanus Smith

Chinajá, 1; 20 km. NNW of Chinajá, 1.

Both individuals were found on the forest floor. An adult male having a total length of 420 mm. has a cream-colored venter with brown flecks. A juvenile having a total length of 172 mm. has a creamy white belly with black crossbands.

At the suggestion of L. C. Stuart, I am following Schmidt (1941:501) in placing *X. mexicanus* as a subspecies of *X. rabdocephalus.*

Micrurus affinis apiatus (Jan)

20 km. NNW of Chinajá, 2; Sayaxché, 1.

All specimens were found beneath litter on the forest floor. All are males having 202 to 211 (average 205) ventrals, 53 to 56 (54.6) caudals, and 34 to 48 (41) primary black rings on the body. There are no yellow rings, and black spots in the red interspaces tend to form secondary black rings (Fig. 6b), the same as in *Pliocercus euryzonus aequalis.* The local name is *coral* or *coralillo.*

Bothrops atrox asper (Garman)

15 km. NW of Chinajá, 1; Sayaxché, 1.

Although we found only two specimens, natives and workmen at the camp at Chinajá stated that the *barba amarilla,* as this snake is known locally, had been abundant when the camp had been established less than two years before our visit.

Bothrops nasutus Bocourt

12 km. NW of Chinajá, 1.

This specimen, a male having a total length of 415 mm., was found on the forest floor. The dorsum is brown with dark brown blotches separated middorsally by a narrow orange-tan stripe extending from the nape to the base of the tail. The belly is grayish tan with white flecks on the lateral edges of the ventrals. The local name is *nahuyaca.*

Bothrops nummifer nummifer (Rüppell)

15 km. NW of Chinajá, 2; Sayaxché, 1.

Two individuals were found on the forest floor, and one adult, having a total length of 953 mm., was removed from the stomach of a large *Drymarchon corais melanurus.* There is considerable variation in color and pattern. A juvenile (KU 58104), having a total length of 332 mm., has a tan dorsum with 19 interconnected dark brown, diamond-shaped, middorsal blotches, the lateral extensions of which are black; the belly is a cream-color with brown squares. An adult female (KU 55706), having a total length of 779 mm., has a dorsal coloration like the preceding specimen, except that the lateral extensions of the dorsal blotches are brown; the belly is a uniform cream-color. A second adult female (KU 55707), having a total length of 953 mm., has a brown dorsum with 21 interconnected black, diamond-shaped, middorsal blotches, the lateral extensions of which are black; the belly is a cream-color with black squares.

The local name for this species is *braza de piedra.*

Bothrops schlegeli schlegeli (Berthold)

Paso Subín, 1.

This specimen was taken from the thatched roof of a house at the edge of the forest and contained the remains of a small mammal. The local name is *nahuyaca.*

HYPOTHETICAL LIST OF SPECIES

Listed below are thirteen species that have not been found in southern El Petén but that probably occur there.

Dermophis mexicanus mexicanus (Duméril and Bibron).—Natives at Chinajá know caecilians, which they call *dos cabezas.* This species has been taken in Tabasco and northern Chiapas. Its occurrence in southern El Petén is expected. Less likely, the caecilian known to the natives at Chinajá is *Gymnopis oligozona,* which is known from Finca Volcán on the southern slopes of the valley of the Río Cahabón in Alta Verapaz.

Gastrophryne elegans (Boulenger).—This small fossorial frog is known from Piedras Negras (Taylor and Smith, 1945:604), 12 miles east of Yaxha (Stuart, 1934:7), and Tikal (Stuart, 1958:18), all in northern and central El Petén. Two specimens in the collection of the University of Kansas are from 28 kilometers northeast of Campur, Alta Verapaz. Probably the species ranges throughout the forested lowlands of northern Alta Verapaz and El Petén.

Mabuya brachypoda Taylor.—The absence of this widespread lizard in our collections cannot be explained. Probably it occurs in southern El Petén, for it is known in northern and central El Petén and in Alta Verapaz.

Dendrophidion vinitor Smith.—This snake is known from Piedras Negras, El Petén and from various localities in Alta Verapaz; it is an inhabitant of humid forest and should occur in southern El Petén.

Elaphe triaspis mutabilis (Cope).—The subspecies *E. triaspis mutabilis* is known from Alta Verapaz and *E. triaspis triaspis* from the Yucatan Peninsula, British Honduras, and Uaxactún in northern El Petén. Because of the much higher degree of resemblance between the faunas of southern El Petén and Alta Verapaz as compared with southern El Petén and Yucatán, *E. triaspis mutabilis* would be expected to occur in southern El Petén.

Ninia diademata nietoi Burger and Werler.—This snake is known from Tikal and from Alta Verapaz; it is a small cryptophile that probably occurs in southern El Petén.

Oxyrhophus petola aequifasciatus Werner.—This snake, which probably is conspecific with *Oxyrhophus baileyi* in southern Veracruz, México, is known from Tikal, British Honduras, and Alta Verapaz; it is expected in southern El Petén.

Pliocercus elapoides salvini Müller.—This species is widespread in the Atlantic lowlands of southern México and nothern Central America; the subspecies *P. elapoides salvini* occurs in Alta Verapaz and probably in southern El Petén.

Rhadinaea decorata decorata (Günther).—This is another small cryptophile that is widespread on the Atlantic lowlands from México to Panamá; it definitely is expected at places like Chinajá in southern El Petén.

Scaphiodontophis annulatus (Duméril and Bibron).—Three subspecies of *Scaphiodontophis annulatus* are recognized in northern Central America: *S. annulatus annulatus* from Alta Verapaz, *S. annulatus hondurensis* from northern Honduras, and *S. annulatus carpicinctus* from Piedras Negras and

Tikal in El Petén and from British Honduras. This rare and highly variable species probably occurs in southern El Petén.

Tantilla schistosa schistosa (Bocourt).—This widespread species in Central America is known from several localities in Alta Verapaz and almost certainly occurs in southern El Petén.

Tropidodipsas sartori sartori Cope.—This fossorial species has been collected in northern El Petén and in Alta Verapaz. The natives at Chinajá described to me a *coral* having orange rings on a black body that likely was this species.

Micrurus elegans veraepacis Schmidt.—This species has been collected at various localities in Alta Verapaz and in Chiapas, inhabits areas like those in southern El Petén, and probably occurs there.

SUMMARY

A study of the amphibians and reptiles in the rainforests of southern El Petén, Guatemala, reveals the presence of 78 species; an additional 13 species probably occur there. In this tropical area having a high amount of rainfall most of the species of amphibians and reptiles have extensive ranges in the wet forests on the Atlantic lowlands of southern México and nothern Central America; some species that more frequently are found in sub-humid forests also occur.

Ecologically the fauna is divided into five major habitats—aquatic, aquatic margin, fossorial, terrestrial, and arboreal. Forty-two per cent of the 78 species are wholly or partly arboreal. The fauna is most closely related to that in Alta Verapaz, Guatemala, but includes many species that occur in the Tikal-Uaxactún area in northeastern Guatemala.

Eleutherodactylus rostralis (Werner) and *E. rhodopis* (Cope) are redefined and their relationships are suggested. The color phases of *Dryadophis melanolomus laevis* and *D. m. alternatus* are discussed; *Dryadophis sanguiventris* Taylor is synonymized with *Dryadophis melanolomus alternatus* (Bocourt).

The breeding habits, eggs, and tadpoles of the hylid frogs *Hyla ebraccata* and *Phyllomedusa callidryas taylori* are described, as are the eggs and juveniles of *Laemanctus deborrei.*

LITERATURE CITED

BAYLOR, E. R. AND STUART, L. C.
1961. A new race of *Bufo valliceps* from Guatemala. Proc. Biol. Soc. Washington, 74:195-202, August 11.

BOGERT, C. M. AND OLIVER, J. A.
1945. A preliminary analysis of the herpetofauna of Sonora. Bull. Amer. Mus. Nat. Hist., 83:297-426, March 30.

BROCCHI, P.
1881-1883. Étude des batraciens de l'Amerique Centrale. Mission scientifique au Mexique. Paris, Imprimerie Nationale, 3 (2):1-122, pls. 1-21.

DUELLMAN, W. E.
1958. A review of the frogs of the genus *Syrrhophus* in western Mexico. Occas. Papers Mus. Zool. Univ. Michigan, 594:1-15, pls. 1-3, June 6.
1960. A distributional study of the amphibians of the Isthmus of Tehuantepec, México. Univ. Kansas Publ. Mus. Nat. Hist., 13:21-72, August 16.
1961. A record size for *Drymarchon corais melanurus*. Copeia, 1960 (4):367-368, January.

DUNN, E. R. AND EMLEN, J. T.
1932. Reptiles and amphibians from Honduras. Proc. Acad. Nat. Sci. Philadelphia, 84:21-32, March 22.

FIRSCHEIN, I. L. AND SMITH, H. M.
1957. A high-crested race of toad (*Bufo valliceps*) and other noteworthy reptiles and amphibians from southern Mexico. Herpetologica, 13:219-222, October 31.

LUNDELL, C. L.
1937. The vegetation of Petén. Carnegie Institute Washington Publ. 178:1-244, pls. 1-39. June 16.

NEILL, W. T. AND ALLEN, R.
1959. Studies on the amphibians and reptiles of British Honduras. Publ. Ross Allen's Reptile Inst., 2:1-76, November 10.

SAPPER, K.
1932. Klimakunde von Mittelamerika. *In* Handbuch Klimakunde, 2:1-74, Taf. 1-13.

SCHMIDT, K. P.
1936. Guatemalan salamanders of the genus *Oedipus*. Zool. Ser. Field Mus. Nat. Hist., 20:135-166, October 31.
1941. The amphibians and reptiles of British Honduras. Zool. Ser. Field Mus. Nat. Hist., 22:475-510, December 30.
1946. Turtles collected by the Smithsonian Biological Survey of the Panamá Canal Zone. Smithsonian Misc. Coll., 106 (8):1-9, pl. 1, August 1.

SIMPSON, G. G.
1960. Notes on the measurement of faunal resemblance. Amer. Jour. Sci., 258-A:300-311.

SMITH, H. M. AND TAYLOR, E. H.
1945. An annotated checklist and key to the snakes of Mexico. Bull. U. S. Natl. Mus., 187: iv + 239 pp., October 5.
1948. An annotated checklist and key to the amphibia of Mexico. Bull. U. S. Natl. Mus., 194: iv + 118 pp., June 17.
1950. An annotated checklist and key to the reptiles of Mexico exclusive of the snakes. Bull. U. S. Natl. Mus., 199: v + 253 pp., October 26.

STUART, L. C.
1934. A contribution to a knowledge of the herpetological fauna of El Peten, Guatemala. Occas. Papers Mus. Zool. Univ. Michigan, 292:1-18, June 29.
1935. A contribution to a knowledge of the herpetology of a portion of the savanna region of central Petén, Guatemala. Misc. Publ. Mus. Zool. Univ. Michigan, 29:1-56, pls. 1-4, October 1.
1937. Some further notes on the amphibians and reptiles of the Peten forest of northern Guatemala. Copeia, 1937 (1):67-70, April 10.
1941a. Studies of Neotropical Colubrinae VIII. A revision of the genus *Dryadophis* Stuart, 1939. Misc. Publ. Mus. Zool. Univ. Michigan, 49:1-105, pls. 1-4, March 19.
1941b. Two new species of *Eleutherodactylus* from Guatemala. Proc. Biol. Soc. Washington, 54:197-200, December 8.

1943. Taxonomic and geographic comments on Guatemalan salamanders of the genus *Oedipus*. Misc. Publ. Mus. Zool. Univ. Michigan, 56:1-33, pls. 1-2, January 30.

1948. The amphibians and reptiles of Alta Verapaz, Guatemala. Misc. Publ. Mus. Zool. Univ. Michigan, 69:1-109, June 12.

1950. A geographic study of the herpetofauna of Alta Verapaz, Guatemala. Contr. Lab. Vert. Biol. Univ. Michigan, 45:1-77, pls. 1-9, May.

1958. A study of the herpetofauna of the Uaxactun-Tikal area of northern El Peten, Guatemala. Contr. Lab. Vert. Biol. Univ. Michigan, 75:1-30, June.

TAYLOR, E. H.

1936. A taxonomic study of the cosmopolitan scincoid lizards of the genus *Eumeces*. Univ. Kansas Sci. Bull., 23:1-643, August 15.

1954. Further studies on the serpents of Costa Rica. Univ. Kansas Sci. Bull., 36:673-801, July 15.

TAYLOR, E. H. AND SMITH, H. M.

1945. Summary of collections of amphibians made in Mexico under the Walter Rathbone Bacon Traveling Scholarship. Proc. U. S. Natl. Mus., 95:521-613, June 30.

Transmitted November 29, 1962.

□

29-5935

(Continued from inside of front cover)

18. Conspecificity of two pocket mice, Perognathus goldmani and P. artus. By E. Raymond Hall and Marilyn Bailey Ogilvie. Pp. 513-518, 1 map. January 14, 1960.
19. Records of harvest mice, Reithrodontomys, from Central America, with description of a new subspecies from Nicaragua. By Sydney Anderson and J. Knox Jones, Jr. Pp. 519-529. January 14, 1960.
20. Small carnivores from San Josecito Cave (Pleistocene), Nuevo León, México. By E. Raymond Hall. Pp. 531-538, 1 figure in text. January 14, 1960.
21. Pleistocene pocket gophers from San Josecito Cave, Nuevo León, México. By Robert J. Russell. Pp. 539-548, 1 figure in text. January 14, 1960.
22. Review of the insectivores of Korea. By J. Knox Jones, Jr., and David H. Johnson. Pp. 549-578. February 23, 1960.
23. Speciation and evolution of the pygmy mice, genus Baimoys. By Robert L. Packard. Pp. 579-670, 4 plates, 12 figures in text. June 16, 1960.

Index. Pp. 671-690

Vol. 10. 1. Studies of birds killed in nocturnal migration. By Harrison B. Tordoff and Robert M. Mengel. Pp. 1-44, 6 figures in text, 2 tables. September 12, 1956.
2. Comparative breeding behavior of Ammospiza caudacuta and A. maritima. By Glen E. Woolfenden. Pp. 45-75, 6 plates, 1 figure. December 20, 1956.
3. The forest habitat of the University of Kansas Natural History Reservation. By Henry S. Fitch and Ronald R. McGregor. Pp. 77-127, 2 plates, 7 figures in text, 4 tables. December 31, 1956.
4. Aspects of reproduction and development in the prairie vole (Microtus ochrogaster). By Henry S. Fitch. Pp. 129-161, 8 figures in text, 4 tables. December 19, 1957.
5. Birds found on the Arctic slope of northern Alaska. By James W. Bee. Pp. 163-211, plates 9-10, 1 figure in text. March 12, 1958.
*6. The wood rats of Colorado: distribution and ecology. By Robert B. Finley, Jr. Pp. 213-552, 34 plates, 8 figures in text, 35 tables. November 7, 1958.
7. Home ranges and movements of the eastern cottontail in Kansas. By Donald W. Janes. Pp. 553-572, 4 plates, 3 figures in text. May 4, 1959.
8. Natural history of the salamander, Aneides hardyi. By Richard F. Johnston and Gerhard A. Schad. Pp. 573-585. October 8, 1959.
9. A new subspecies of lizard, Cnemidophorus sacki, from Michoacán, México. By William E. Duellman. Pp. 587-598, 2 figures in text. May 2, 1960.
10. A taxonomic study of the middle American snake, Pituophis deppei. By William E. Duellman. Pp. 599-610, 1 plate, 1 figure in text. May 2, 1960.

Index. Pp. 611-626.

Vol. 11. Nos. 1-10 and index. Pp. 1-703, 1958-1960.

Vol. 12. 1. Functional morphology of three bats: Sumops, Myotis, Macrotus. By Terry A. Vaughan. Pp. 1-153, 4 plates, 24 figures in text. July 8, 1959.
*2. The ancestry of modern Amphibia: a review of the evidence. By Theodore H. Eaton, Jr. Pp. 155-180, 10 figures in text. July 10, 1959.
3. The baculum in microtine rodents. By Sydney Anderson. Pp. 181-216, 49 figures in text. February 19, 1960.
*4. A new order of fishlike Amphibia from the Pennsylvanian of Kansas. By Theodore H. Eaton, Jr., and Peggy Lou Stewart. Pp. 217-240, 12 figures in text. May 2, 1960.
5. Natural history of the bell vireo. By Jon C. Barlow. Pp. 241-296, 6 figures in text. March 7, 1962.
6. Two new pelycosaurs from the lower Permian of Oklahoma. By Richard C. Fox. Pp. 297-307, 6 figures in text. May 21, 1962.
7. Vertebrates from the barrier island of Tamaulipas, México. By Robert K. Selander, Richard F. Johnston, B. J. Wilks, and Gerald G. Raun. Pp. 309-345, pls. 5-8. June 18, 1962.
8. Teeth of Edestid sharks. By Theodore H. Eaton, Jr. Pp. 347-362, 10 figures in text. October 1, 1962.

More numbers will appear in volume 12.

Vol. 13. 1. Five natural hybrid combinations in minnows (Cyprinidae). By Frank B. Cross and W. L. Minckley. Pp. 1-18. June 1, 1960.
2. A distributional study of the amphibians of the Isthmus of Tehuantepec, México. By William E. Duellman. Pp. 19-72, pls. 1-8, 3 figures in text. August 16, 1960.
3. A new subspecies of the slider turtle (Pseudemys scripta) from Coahulia, México. By John M. Legler. Pp. 73-84, pls. 9-12, 3 figures in text. August 16, 1960.
4. Autecology of the copperhead. By Henry S. Fitch. Pp. 85-288, pls. 13-20, 26 figures in text. November 30, 1960.
5. Occurrence of the garter snake, Thamnophis sirtalis, in the Great Plains and Rocky Mountains. By Henry S. Fitch and T. Paul Maslin. Pp. 289-308, 4 figures in text. February 10, 1961.
6. Fishes of the Wakarusa river in Kansas. By James E. Deacon and Artie L. Metcalf. Pp. 309-322, 1 figure in text. February 10, 1961.
7. Geographic variation in the North American cyprinid fish, Hybopsis gracilis. By Leonard J. Olund and Frank B. Cross. Pp. 323-348, pls. 21-24, 2 figures in text. February 10, 1961.

(Continued on outside of back cover)

(Continued from inside of back cover)

8. Decriptions of two species of frogs, genus Ptychohyla; studies of American hylid frogs, V. By William E. Duellman. Pp. 349-357, pl. 25, 2 figures in text. April 27, 1961.
9. Fish populations, following a drought, in the Neosho and Marais des Cygnes rivers of Kansas. By James Everett Deacon. Pp. 359-427, pls. 26-30, 3 figs. August 11, 1961.
10. Recent soft-shelled turtles of North America (family Trionychidae). By Robert G. Webb. Pp. 429-611, pls. 31-54, 24 figures in text. February 16, 1962.

Index. Pp. 613-624.

Vol. 14. 1. Neotropical bats from western México. By Sydney Anderson. Pp. 1-8. October 24, 1960.
2. Geographic variation in the harvest mouse. Reithrodontomys megalotis, on the central Great Plains and in adjacent regions. By J. Knox Jones, Jr., and B. Mursaloglu. Pp. 9-27, 1 figure in text. July 24, 1961.
3. Mammals of Mesa Verde National Park, Colorado. By Sydney Anderson. Pp. 29-67, pls. 1 and 2, 3 figures in text. July 24, 1961.
4. A new subspecies of the black myotis (bat) from eastern Mexico. By E. Raymond Hall anad Ticul Alvarez. Pp. 69-72, 1 figure in text. December 29, 1961.
5. North American yellow bats, "Dasypterus," and a list of the named kinds of the genus Lasiurus Gray. By E. Raymond Hall and J. Knox Jones, Jr. Pp. 73-98, 4 figures in text. December 29, 1961.
6. Natural history of the brush mouse (Peromyscus boylii) in Kansas with description of a new subspecies. By Charles A. Long. Pp. 99-111, 1 figure in text. December 29, 1961.
7. Taxonomic status of some mice of the Peromyscus boylii group in eastern Mexico, with description of a new subspecies. By Ticul Alvarez. Pp. 113-120, 1 figure in text. December 29, 1961.
8. A new subspecies of ground squirrel (Spermophilus spilosoma) from Tamaulipas, Mexico. By Ticul Alvarez. Pp. 121-124. March 7, 1962.
9. Taxonomic status of the free-tailed bat, Tadarida yucatanica Miller. By J. Knox Jones, Jr., and Ticul Alvarez. Pp. 125-133, 1 figure in text. March 7, 1962.
10. A new doglike carnivore, genus Cynaretus, from the Clarendonian Pliocene, of Texas. By E. Raymond Hall and Walter W. Dalquest. Pp. 135-138, 2 figures in text. April 30, 1962.
11. A new subspecies of wood rat (Neotoma) from northeastern Mexico. By Ticul Alvarez. Pp. 139-143. April 30, 1962.
12. Noteworthy mammals from Sinaloa, Mexico. By J. Knox Jones, Jr., Ticul Alvarez, and M. Raymond Lee. Pp. 145-159, 1 figure in text. May 18, 1962.
13. A new bat (Myotis) from Mexico. By E. Raymond Hall. Pp. 161-164, 1 figure in text. May 21, 1962.
14. The mammals of Veracruz. By E. Raymond Hall anad Walter W. Dalquest. Pp. 165-362, 2 figures. May 20, 1963.
15. The recent mammals of Tamaulipas, México. By Ticul Alvarez. Pp. 363-473, 5 figures in text. May 20, 1963.

More numbers will appear in volume 14.

Vol. 15. 1. The amphibians and reptiles of Michoacán, México. By William E. Duellman. Pp. 1-148, pls. 1-6, 11 figures in text. December 20, 1961.
2. Some reptiles and amphibians from Korea. By Robert G. Webb, J. Knox Jones, Jr., and George W. Byers. Pp. 149-173. January 31, 1962.
3. A new species of frog (Genus Tomodactylus) from western México. By Robert G. Webb. Pp. 175-181, 1 figure in text. March 7, 1962.
4. Type specimens of amphibians and reptiles in the Museum of Natural History, the University of Kansas. By William E. Duellman and Barbara Berg. Pp. 183-204. October 26, 1962.
5. Amphibians and Reptiles of the Rainforests of Southern El Petén, Guatemala. By William E. Duellman. Pp. 205-249, pls. 7-10, 6 figures in text. October 4, 1963.

More numbers will appear in volume 15.

COMP. ZOOL.
LIBRARY
OCT 11 19
HARVARD
UNIVERSITY

UNIVERSITY OF KANSAS PUBLICATIONS
MUSEUM OF NATURAL HISTORY

Volume 15, No. 6, pp. 251-295, 9 figs.
October 4, 1963

A Revision of Snakes of the Genus Conophis (Family Colubridae, from Middle America)

BY

JOHN WELLMAN

UNIVERSITY OF KANSAS
LAWRENCE
1963

UNIVERSITY OF KANSAS PUBLICATIONS
MUSEUM OF NATURAL HISTORY

Institutional libraries interested in publications exchange may obtain this series by addressing the Exchange Librarian, University of Kansas Library, Lawrence, Kansas. Copies for individuals, persons working in a particular field of study, may be obtained by addressing instead the Museum of Natural History, University of Kansas, Lawrence, Kansas. There is no provision for sale of this series by the University Library, which meets institutional requests, or by the Museum of Natural History, which meets the requests of individuals. However, when individuals request copies from the Museum, 25 cents should be included, for each separate number that is 100 pages or more in length, for the purpose of defraying the costs of wrapping and mailing.

* An asterisk designates those numbers of which the Museum's supply (not the Library's supply) is exhausted. Numbers published to date, in this series, are as follows:

Vol. 1. Nos. 1-26 and index. Pp. 1-638, 1946-1950.

*Vol. 2. (Complete) Mammals of Washington. By Walter W. Dalquest. Pp. 1-444, 140 figures in text. April 9, 1948.

Vol. 3. *1. The avifauna of Micronesia, its origin, evolution, and distribution. By Rollin H. Baker. Pp. 1-359, 16 figures in text. June 12, 1951.
*2. A quantitative study of the nocturnal migration of birds. By George H. Lowery, Jr. Pp. 361-472, 47 figures in text. June 29, 1951.
3. Phylogeny of the waxwings and allied birds. By M. Dale Arvey. Pp. 473-530, 49 figures in text, 13 tables. October 10, 1951.
*4. Birds from the state of Veracruz, Mexico. By George H. Lowery, Jr., and Walter W. Dalquest. Pp. 531-649, 7 figures in text, 2 tables. October 10, 1951.
Index. Pp. 651-681.

*Vol. 4. (Complete) American weasels. By E. Raymond Hall. Pp. 1-466, 41 plates, 31 figures in text. December 27, 1951.

Vol. 5. Nos. 1-37 and index. Pp. 1-676, 1951-1953.

*Vol. 6. (Complete) Mammals of Utah, *taxonomy and distribution.* By Stephen D. Durrant. Pp. 1-549, 91 figures in text, 30 tables. August 10, 1952.

Vol. 7. Nos. 1-15 and index. Pp. 1-651, 1952-1955.

Vol. 8. Nos. 1-10 and index. Pp. 1-675, 1954-1956.

Vol. 9. *1. Speciation of the wandering shrew. By James S. Findley. Pp. 1-68, 18 figures in text. December 10, 1955.
2. Additional records and extension of ranges of mammals from Utah. By Stephen D. Durrant, M. Raymond Lee, and Richard M. Hansen. Pp. 69-80. December 10, 1955.
3. A new long-eared myotis (Myotis evotis) from northeastern Mexico. By Rollin H. Baker and Howard J. Stains. Pp. 81-84. December 10, 1955.
4. Subspeciation in the meadow mouse, Microtus pennsylvanicus, in Wyoming By Sydney Anderson. Pp. 85-104, 2 figures in text. May 10, 1956.
5. The condylarth genus Ellipsodon. By Robert W. Wilson. Pp. 105-116, 6 figures in text. May 19, 1956.
6. Additional remains of the multituberculate genus Eucosmodon. By Robert W. Wilson. Pp. 117-123, 10 figures in text. May 19, 1956.
7. Mammals of Coahulia, Mexico. By Rollin H. Baker. Pp. 125-335, 75 figures in text. June 15, 1956.
8. Comments on the taxonomic status of Apodemus peninsulae, with description of a new subspecies from North China. By J. Knox Jones, Jr. Pp. 337-346, 1 figure in text, 1 table. August 15, 1956.
9. Extensions of known ranges of Mexican bats. By Sydney Anderson. Pp. 347-351. August 15, 1956.
10. A new bat (Genus Leptonycteris) from Coahulia. By Howard J. Stains. Pp. 353-356. January 21, 1957.
11. A new species of pocket gopher (Genus Pappogeomys) from Jalisco, Mexico. By Robert J. Russell. Pp. 357-361. January 21, 1957.
12. Geographic variation in the pocket gopher, Thomomys bottae, in Colorado. By Phillip M. Youngman. Pp. 363-387, 7 figures in text. February 21, 1958.
13. New bog lemming (genus Synaptomys) from Nebraska. By J. Knox Jones, Jr. Pp. 385-388. May 12, 1958.
14. Pleistocene bats from San Josecito Cave, Nuevo León, México. By J. Knox Jones, Jr. Pp. 389-396. December 19, 1958.
15. New subspecies of the rodent Baiomys from Central America. By Robert L. Packard. Pp. 397-404. December 19, 1958.
16. Mammals of the Grand Mesa, Colorado. By Sydney Anderson. Pp. 405-414, 1 figure in text, May 20, 1959.
17. Distribution, variation, and relationships of the montane vole, Microtus montanus. By Sydney Anderson. Pp. 415-511, 12 figures in text, 2 tables. August 1, 1959.

(Continued on inside of back cover)

University of Kansas Publications
Museum of Natural History

Volume 15, No. 6, pp. 251-295, 9 figs.
October 4, 1963

A Revision of Snakes of the Genus Conophis (Family Colubridae, from Middle America)

BY

JOHN WELLMAN

University of Kansas
Lawrence
1963

University of Kansas Publications, Museum of Natural History
Editors: E. Raymond Hall, Chairman, Henry S. Fitch,
Theodore H. Eaton, Jr.

Volume 15, No. 6, pp. 251-295, 9 figs.
Published October 4, 1963

University of Kansas
Lawrence, Kansas

PRINTED BY
JEAN M. NEIBARGER, STATE PRINTER
TOPEKA, KANSAS
1963

29-5936

A Revision of Snakes of the Genus Conophis (Family Colubridae, from Middle America)

BY

JOHN WELLMAN

CONTENTS

PAGE

INTRODUCTION 253
ACKNOWLEDGMENTS 254
MATERIALS AND METHODS 254
GENUS Conophis Peters 255
Key to the Species and Subspecies 257
Analysis of Characters 257
Scutellation 258
Size and Proportions 258
Color Pattern 260
Sexual Dimorphism 260
C. lineatus 262
C. lineatus dunni 262
C. lineatus lineatus 267
C. lineatus concolor 270
C. nevermanni 272
C. pulcher 274
C. vittatus 277
Skull 282
Dentition 288
Vertebrae 288
Hemipenes 289
Food and Feeding 289
Effect of Poison 290
TAXONOMIC RELATIONSHIPS AND EVOLUTION 291
SUMMARY 292
LITERATURE CITED 293

INTRODUCTION

Need for a comprehensive systematic review of the snakes of the genus *Conophis* was pointed out by Stuart (1954a, b). Since these snakes appeared to be of zoogeographic importance in the Central American region, I undertook the review as set forth on the following pages.

ACKNOWLEDGMENTS

For permission to examine specimens, and for information concerning specimens in their care, I am grateful to Mr. L. C. Battersby and Miss Alice G. C. Grandison, British Museum (Natural History); Mr. Charles M. Bogert and Dr. Richard G. Zweifel, American Museum of Natural History; Dr. Doris M. Cochran, United States National Museum; Prof. William B. Davis, Agricultural and Mechanical College of Texas; Dr. Josef Eiselt, Naturhistorisches Museums, Vienna; Prof. Norman Hartweg and Prof. Laurence C. Stuart, Museum of Zoology, University of Michigan; Dr. Robert F. Inger, Chicago Natural History Museum; Dr. Alan E. Leviton, California Academy of Sciences; Mr. Edmond V. Malnate, Academy of Natural Sciences, Philadelphia; Prof. George S. Myers, Stanford University Natural History Museum; Mr. Wilfred T. Neill, Ross Allen's Reptile Institute; Mr. Neil D. Richmond, Carnegie Museum; Dr. William J. Riemer, University of Florida Collections; Prof. Robert C. Stebbins, Museum of Vertebrate Zoology, University of California; Prof. Hobart M. Smith, University of Illinois Natural History Museum; and Dr. Ernest E. Williams, Museum of Comparative Zoology, Harvard.

Prof. William E. Duellman supplied invaluable information and guidance in my study. I am grateful to Prof. E. Raymond Hall for use of facilities of the Museum of Natural History and editorial assistance. I thank Prof. Laurence C. Stuart and Prof. Edward H. Taylor for information and suggestions. My own field experience in Middle America came as a result of assisting Professor Duellman in his own researches supported by a grant from the National Science Foundation (NSF-G 9827). For these things I am deeply grateful. Specimens that I have seen alive were collected by field companions Dale L. Hoyt and Jerome B. Tulecke. Finally, I am grateful to my wife, Margaret L. Wellman, for much help including typing much of the manuscript.

MATERIALS AND METHODS

Of the 325 specimens of the genus *Conophis* available to me, representing most of those in museum collections, scale counts were made in the usual manner on 309. Ventrals were counted following the system proposed by Dowling (1951:97-99); the anal plate was not included. The anteroposterior position of the place where reduction occurs in the number of the dorsal rows of scales is designated by citing the number of the ventral scale directly beneath that place.

Measurements were taken to the nearest millimeter by means of a millimeter stick. Body length is the distance from the tip of the snout to the posterior edge of the anal plate; tail length, from the latter point to the tip of the tail; and total length, the sum of the body plus tail.

Descriptions of color are based on preserved specimens. Where descriptions of the color of living individuals are given, the data were taken from Kodachrome slides made available to me by William E. Duellman. Due to the transient nature of the longitudinal dark stripes in these snakes, no standard terminology has been devised, except that the posterior continuations of the stripes which on the head pass through the eye are termed lateral stripes; the posterior continuations of the median stripe of the head are termed dorso-

lateral stripes. A paravertebral stripe is one that is present on the scale-row on either side, of, but not including, the mid-dorsal (vertebral) scale-row.

In order to reduce confusion in the discussion of variation, the numbers designating the rows of dorsal scales are written as 1st, 2nd, whereas the numbers designating the stripes are written as first, second.

Except in three dried skeletons, teeth were counted on dentigerous bones *in situ*. Since teeth are often missing, the sockets were counted in order to obtain an accurate count.

In accounts of the species and subspecies, the observed range of variation is followed by the mean in parentheses; in some instances the mean is followed by the standard deviation, also in parentheses. An example is 65-79 (70.6±3.93).

Each synonymy includes all generic and specific combinations known to me that have been used for the genus, and, in addition, references to catalogues, checklists, and reports of collections.

Localities of occurrence that are not plotted on the distribution maps are recorded in italic type under Specimens Examined. In the list of Specimens Examined the localities and specimens are listed in the following order: countries in alphabetical order; states or departments in alphabetical order in each country; localities in alphabetical order in each state or department; museum numbers in numerical order after the abbreviations of names of museums. When more than one specimen bears a single catalogue number, the number of specimens is given in parentheses following the museum catalogue number. Specimens for which data are given only as to country or to state or department are listed first after the name of that political unit under "no specific locality."

The abbreviations for the museum collections are:

AMNH	American Museum of Natural History
ANSP	Academy of Natural Sciences of Philadelphia
BMNH	British Museum (Natural History)
CAS	California Academy of Sciences
CNHM	Chicago Natural History Museum
ERA-WTN	E. Ross Allen-Wilfred T. Neill, Ross Allen's Reptile Institute
KU	University of Kansas Museum of Natural History
MCZ	Museum of Comparative Zoology, Harvard
MVZ	Museum of Vertebrate Zoology, University of California
NMW	Naturhistorisches Museums Wien, Vienna
SU	Stanford University Natural History Museum
TCWC	Texas Cooperative Wildlife Collection, Agricultural and Mechanical College of Texas
UF	University of Florida Collections
UIMNH	University of Illinois Museum of Natural History
UMMZ	University of Michigan Museum of Zoology
USNM	United States National Museum

Family COLUBRIDAE

Subfamily Xenodontinae

Genus Conophis Peters

Tomodon (part) Duméril, Bibron and Duméril, Érpétologie Générale, 7(pt.2):936, February 25, 1854 (*lineatus* and *vittatus*); Salvin, Proc. Zool. Soc. London, 28:455, 1860 (*pulcher*).

Psammophis (part), Günther, Catalogue of Colubrine Snakes in the Collection of the British Museum, London, 1858:135 (*lineatus*).

Conophis Peters, Monatsb. Akad. Wiss. Berlin, 1860:519-520, pl., fig. 3 (*vittatus*); Cope, Proc. Acad. Nat. Sci. Philadelphia, 13:300, December 28, 1861 (*lineatus concolor*); Proc. Acad. Nat. Sci. Philadelphia, 18:318-319, February 20, 1867 (*lineatus concolor*); Proc. Acad. Nat. Sci. Philadelphia, ser. 2, 8:137, 1876 (*pulcher*); Bocourt in Duméril, Bocourt and Mocquard, Mission Scientifique au Mexique et dans l'Amerique Centrale, 2:643-644, pl. 38, fig. 5, 1886 (*lineatus lineatus*); Cope, Proc. Amer. Philos. Soc., 23:489, October 28, 1886; Hoffmann, Klassen und Ordnungen des Thier-Reichs. Reptilien. Bd. 6, 3:1707, 1890; Cope, Trans. Amer. Philos. Soc., 18:207, April 15, 1895; Dunn, Bull. Antivenin Inst. Amer., 2(1):21, 24, April, 1928; Copeia, no. 4:214, December 31, 1937 (*nevermanni*).

Tachymenis (in part), Garman, Bull. Essex Inst., 16:33, January 9, 1884 (*vittatus* and *lineatus*).

Erythrolamprus (in part), Ditmars, Bull. Antivenin Inst. Amer., 2(2):27-29, June.

Coniophanes (in part), Wettstein, Sitz. Akad. Wiss. Wien, mathem-naturw. kl. 143:37-38, 1934 (*nevermanni*).

Historical summary.—In 1854 Duméril, Bibron and Duméril described and figured *Tomodon lineatum* from America. In 1860 Peters described and figured as a new genus and species, *Conophis vittatus*, based on a specimen that he had obtained from a dealer in Hamburg. The provenance of this specimen is not known, for it was discovered aboard a ship near the mouth of the Mississippi River. It was not until 1871 that Cope included *lineatus* in the genus *Conophis*. Cope (1861) proposed the name *Conophis vittatus* (*nec* Peters, 1860). Later (1900) he changed its name to *Conophis lineaticeps*. Early uncertainty of the relationships of the species *lineatus* caused Günther (1858) to place it in the genus *Psammophis*. With the exception of Garman (1884a and 1884b) who placed *lineatus* in the genus *Tachymenis*, and Wettstein (1934) who reported five specimens of *Conophis nevermanni* as *Coniophanes i. imperialis*, all specimens reported after 1876 were placed in the genus *Conophis*.

The only previous attempt to review the systematics of this genus was made by Smith (1941) who based his study primarily on specimens in the United States National Museum. He examined only 28 specimens, including none of one species (*nevermanni*).

Description.—Hemipenis slightly bifurcate having forked sulcus spermaticus, large spines near base, and smaller spines or papillae on flounces nearer apices; prediastemal maxillary teeth 8-12, subequal in length, and followed by short diastema and one enlarged fang or two; fangs grooved, only one functional at any one time, unless snake is in process of shedding teeth; teeth 6-10 on palatine, 15 to 19 on pterygoid, 15 to 21 on dentary; teeth on dentary decreasing in size posteriorly; large parotid (venom) gland on either side of head in temporal region; head shields of basically unmodified colubrid type excepting decurved rostral; rostral concave below and therein modified for burrowing; internasals and prefrontals paired; nasals divided; loreal single; preocular one, rarely two; postoculars, two; supralabials, 7-8, 3rd and 4th or 4th and 5th under eye; infralabials, 8-11, usually 9 or 10; temporals, normally 1 plus 2 plus 3; chin-shields subequal in length; ventrals, 149-183, rounded and overlapping; caudals, 55-89, paired and imbricate; anal divided; dorsal

scales smooth and in 19 rows at mid-body with no apical pits or keels; scale reduction normally involving fusion of 3rd and 4th rows, resulting in 17 scale-rows near tail; tail length more than 20 per cent of body length; maximum total length exceeding 1.1 meters; dorsal color pattern consisting of dark stripes, or no darkening, on paler ground-color; ventral surfaces immaculate pale yellowish or white, except on specimens having single lateral dark spots on some or all ventrals; pupil round; diurnal or crepuscular; feeding primarily on small lizards, sometimes on small mammals or other snakes.

Distribution.—Semiarid regions of southern México and Central America as far south as Costa Rica.

KEY TO THE SPECIES AND SUBSPECIES

Although many juveniles differ greatly in general coloration from the adults, both the juveniles and the adults of any species or subspecies can be identified from the following key; juveniles differ from adults in extent and intensity of dark pigmentation but not in rows of scales involved.

1. Seven supralabials (3rd and 4th below orbit); 3 to 8 dark stripes along body 2
   Eight supralabials (4th and 5th below orbit); unstriped or with more than 4 dark stripes along body, or dark with 2 or 4 pale stripes 3
2. Dark stripes involving no more than one longitudinal scale-row ..... *C. lineatus lineatus* (part), p. 267
   Dark stripes involving at least two adjacent scale-rows ... *C. vittatus*, p. 277
3. Supralabials having black borders above; head and body generally black with 2 or 4 white lines running length of body ..... *C. nevermanni*, p. 272
   Supralabials immaculate or having dark borders below; head and body usually pale with dark stripes, or without stripes 4
4. Lateral dark stripe through eye involving upper half of second scale-row; dark stripe on paravertebral row, at least posteriorly ..... *C. pulcher*, p. 274
   Lateral dark stripe becoming indistinct on body, or restricted to 4th or 3rd and 4th rows anteriorly, not involving 2nd scale-row on anterior ⅓ of body (an auxiliary lateral stripe sometimes present involving 2nd row); no paravertebral stripes 5
5. Stripes disappearing posteriorly (except for small spots of pigment on scale-row 4 or 7); 1st scale-row unpigmented ... *C. lineatus concolor*, p. 270
   Stripes present posteriorly; 1st scale-row pigmented 6
6. Lateral stripes narrow on nape, restricted to 4th scale-row on body ..... *C. lineatus lineatus* (part), p. 267
   Lateral stripes involving 3rd and 4th rows, at least on nape ..... *C. lineatus dunni*, p. 262

Analysis of Characters

Characters showing inter-specific and intra-specific variation and that have a wide range of variation were analyzed statistically, when possible, in order to determine extent of variation. One character (see table 3) was analyzed for sexual dimorphism, and for it the coefficient of difference is also given. The statistical terms and formulae have been adopted from Mayr, Linsley and Usinger (1953). Dorsal head shields varied individually and were of no taxonomic importance. Osteological and hemipeneal characters did not show enough variation to be considered here.

Scutellation

Labials, dorsals, ventrals, and subcaudals were the most useful scales.

Labials.—All species usually have eight supralabials except *C. vittatus,* which has seven. The only other population having a relatively high frequency of occurrence of seven supralabials is *C. l. lineatus.* In specimens having eight supralabials, the fourth and fifth enter the orbit; in specimens having seven supralabials, the third and fourth enter the orbit (the second and third are fused). Usually there are ten infralabials, sometimes nine or eleven; specimens having seven supralabials usually have nine infralabials, sometimes eight, rarely ten.

Dorsals.—Although there is no variation in the number of rows of dorsal scales, there is some in the method of scale reduction. There are 19 rows of dorsal scales from close behind the head to about midway on the body where two rows are lost, leaving 17 rows from there to near the base of the tail. This reduction is accomplished by fusion of the scales of the 3rd and 4th rows or sometimes by the dropping out of the 3rd row. The place at which reduction occurs in number of dorsal scales in relation to the ventral (scale) directly below is highly variable and of little taxonomic importance (table 1).

TABLE 1.—VARIATION IN THE PLACE OF DORSAL SCALE REDUCTION IN CONOPHIS.

Taxon	Number of Specimens	Range	Mean	Standard Deviation	Standard Error	Coefficient of Variation
l. concolor	45	89–114	102.5	5.57	0.83	5.43
l. dunni	36	91–111	102.1	4.59	0.77	4.50
l. lineatus	26	91–107	100.2	3.59	0.72	3.58
nevermanni	6	84– 97	93.2	4.71	1.92	5.05
pulcher	26	94–119	104.6	4.90	0.96	4.68
vittatus	170	84–118	102.3	6.60	0.16	6.45

Ventrals.—The number of ventral scutes varies from 149-183, and shows no significant variation in the means (table 2).

Subcaudals.—The number of subcaudal scutes varies from 55 to 89. In some populations there is no overlap in the range of variation of males and females. The total variation and sexual dimorphism are analyzed in table 3.

Size and Proportions

Although considerable variation in size is observable, little taxonomic use is made of size since sufficient series are not available to determine age classes. The subspecies attaining the largest size is *C. lineatus concolor;* all others are smaller and of about the same size and proportions. The longest specimen, a male of *C. l. concolor,* has a body length of 893 mm., a tail length of 274 mm., and a total length of 1167 mm.

TABLE 2.—VARIATION IN THE NUMBER OF VENTRALS IN CONOPHIS.

Taxon	Number of Specimens	Range	Mean	Standard Deviation	Standard Error	Coefficient of Variation
l. concolor	45	158–170	163.7	1.56	0.23	0.95
l. dunni	36	159–178	167.2	4.56	0.76	2.72
l. lineatus	26	157–169	163.5	3.59	0.72	2.20
nevermanni	6	173–183	176.5	4.00	1.63	2.27
pulcher	26	149–180	169.5	5.31	1.04	3.13
vittatus	171	149–180	163.7	6.33	0.15	3.87

TABLE 3.—SEXUAL DIMORPHISM AS INDICATED BY VARIATION IN THE NUMBER OF SUBCAUDALS IN CONOPHIS.

Taxon	Sex	Number of Specimens	Range	Mean	Standard Deviation	Standard Error	Coefficient of Variation	Coefficient of Difference
lineatus concolor	♂	22	68–74	70.3	2.14	0.46	3.04	1.97
	♀	16	56–65	61.8	2.18	0.55	3.53	
lineatus dunni	♂	14	67–80	74.5	3.86	1.03	5.18	0.95
	♀	16	60–72	67.1	3.91	0.97	5.82	
lineatus lineatus	♂	11	67–73	69.8	6.17	1.85	8.84	0.60
	♀	9	60–66	62.4	6.17	2.06	9.89	
nevermanni	♂	3	82–89	85.3	.....	.....	.....	.....
	♀	2	71–76	73.5	.....	.....	.....	
pulcher	♂	7	70–79	74.3	3.11	1.17	4.19	0.93
	♀	11	65–71	68.2	3.42	1.08	5.01	
vittatus	♂	95	59–76	67.8	3.33	0.34	4.91	1.28
	♀	58	55–66	60.0	2.75	0.36	4.58	

Color Pattern

This is the primary feature used to separate species and subspecies in this genus. The color pattern consists of three black or deep brown stripes on the dorsal part of the head, one mid-dorsally, and one on each side of the head passing through the eye. On the body, there are usually dark longitudinal stripes on a pale tan or white background. There may be as few as three in *vittatus*, and as many as 13 in *l. dunni;* except that there is none in *C. l. concolor*. There are two pairs of primary dark stripes. The first is the body stripe that is the posterior extension of the stripe which on the head passes through the eye and is termed the lateral stripe. The other primary stripe is the posterior continuation of the mid-dorsal head stripe. Usually it is split into two dorsolateral stripes on the body. Stripes may be present on the scale-row to either side of the primary stripe. These stripes are usually dark brown or black and are the secondary stripes. Finally, additional stripes may be present that are paler brown and bear no direct relationship to the primary stripes. These are auxiliary stripes.

Every stripe originates either as broad continuous stripe or as a row of spots or dashes, forming a discontinuous stripe, which in some specimens becomes continuous posteriorly. The stripes are usually black or deep brown, although auxiliary stripes are sometimes paler. The dorsal ground color is pale brown, tan, olive, or white; usually the ground color is palest ventrally and darkest dorsally.

In some specimens of *Conophis* the lateral tips of the ventrals are spotted, one spot on each end of each ventral. Otherwise, the ventrals are immaculate white.

In some species there is considerable ontogenetic change in color pattern, although the juveniles bear the basic color characteristics of the adults. For example, juveniles of the sympatric species *C. lineatus dunni* and *C. pulcher* can be separated on the basis of which scale-rows are darkly pigmented. *C. l. dunni* has eight stripes in juveniles and as many as 13 in adults. Juveniles show a greater contrast between the black stripes and the pale ground color than do adults. With increased age (size) the stripes in some populations become paler and are split; simultaneously the ground color becomes darker.

Sexual Dimorphism

Sexual dimorphism is evident in all species and subspecies of *Conophis*. Differences always exist in the number of subcaudals and in the tail/body ratio; males have more subcaudals and relatively longer tails than do females (table 3). Otherwise, there is little sexual dimorphism in these snakes. Males and females cannot be differentiated by any feature of coloration.

Formulation of a biological concept of the species as defined by Mayr (1942) is difficult when most of the data primarily relied upon are from preserved specimens. Nevertheless, a total view of variation was attempted so that differences within and between populations could be recognized. Differences, between popula-

tions, that seem to be part of a continuous or internal cline (Huxley, 1942) are not used for characterizing subspecies.

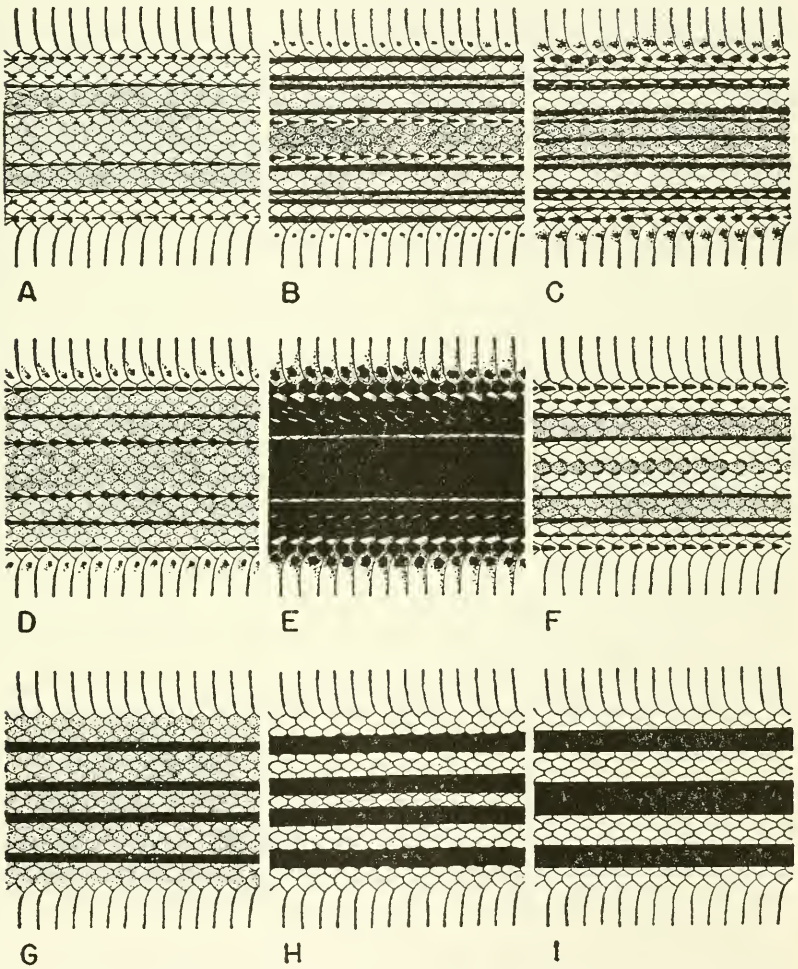


FIG. 1. Patterns of dorsal coloration at mid-body of adults of all species and subspecies of the genus *Conophis* except *C. lineatus concolor.* A. *C. lineatus dunni* (UMMZ 107339) from Santa Rosa, Guatemala. B. C. *lineatus dunni* (UMMZ 116537) from 1.5 mi. N Matagalpa, Nicaragua. C. *C. lineatus dunni* (ANSP 3480) from "San Jose," Costa Rica. D. *C. l. lineatus* (KU 23253) from Río Blanco, 20 km. WNW Piedras Negras, Veracruz, México. E. *C. nevermanni* (ANSP 22424) "San Jose," Costa Rica. F. *C. pulcher* (UIMNH 33646) from Soconusco, Chiapas, México. G. *C. vittatus* (KU 39626) from Atencingo, Puebla, México. H. *C. vittatus* (TCWC 9473) from 1 mi. S Colotlipa, Guerrero, México. I. *C. vittatus* (UMMZ 82653) from "vicinity of" Salina Cruz, Oaxaca, México. Approximately × ¾.

Conophis lineatus (Duméril, Bibron and Duméril)

Tomodon lineatum (in part) Duméril, Bibron and Duméril, Érpétologie Générale, 7(pt. 2):936-938, February 25, 1854.

Diagnosis.—No dark pigmentation posterior to nape; lateral dark stripe anteriorly passing through eye and posteriorly involving 4th or 3rd and 4th scale-rows only; first scale-row darkly pigmented; no paravertebral dark stripe; six to thirteen (or no) dark stripes at mid-body; usually eight (sometimes seven) supralabials immaculate white or having dark ventral margins.

Variation.—The variation in this species is discussed more completely in the descriptions of the subspecies. One hundred and seven specimens have 157 to 178 (164.8) ventrals. Eighty-eight of these snakes having complete tails have 56 to 80 (68.0) subcaudals; the number of ventrals plus subcaudals varies from 222 to 247 (233.5) in 87 of these. On 107 specimens the reduction from 19 to 17 dorsal scale-rows takes place between ventrals 89 and 114 (101.8). Sexual dimorphism is evident in the number of subcaudals; there are, on the average, fewer subcaudals in females than in males of each subspecies. The largest specimen is a male *C. l. concolor* (USNM 46345) from Chichén Itzá, Yucatán, México, having a body length of 893 mm., a tail length of 274 mm. and a total length of 1167 mm. The smallest is a juvenile *C. l. dunni* (MCZ 49749) from Tegucigalpa, Honduras, having a body length of 162 mm., a tail length of 51 mm. and a total length of 213 mm.

The greatest variation is in coloration. Dark color, or lack thereof has been used to separate the subspecies of *C. lineatus.* The ground-color is pale brown, pale olive or white, either with no stripes on the body or with eight to thirteen dark stripes at mid-body. Specimens having dark stripes on the body always have black or dark brown pigmentation on the first, 4th and 7th dorsal scale-rows. In some there is dark pigmentation on the 2nd, 3rd, 8th and 10th rows of scales. The stripes appear on the nape or farther posteriorly, usually on the anterior third of the body, either as a series of spots or dashes that form a continuous stripe farther posteriorly or as a continuous stripe.

The ventrals usually have more or less conspicuous dark spots laterally on those specimens having dark stripes present on the dorsum; spots are absent on all specimens having no dorsal stripes and on some specimens having dorsal stripes. Except for the dark lateral spots (when present) the ventrals are immaculate white. Usually the dorsal ground-color is pale tan, especially on the striped forms. The ground-color is usually palest on the lower dorsal scale rows and darkest dorsally.

Three populations are separable as subspecies; one has no stripes on the body and occurs in the Yucatán Peninsula. The other two have stripes on the dorsum and vary clinally in coloration from the north (Veracruz, México) to south (Costa Rica) (Fig. 2). Reasons for separating these widespread, variable snakes into two subspecies are that they are discontinuous in distribution (the population in Veracruz is disjunct from the one that extends from Guatemala to Costa Rica), and that these populations have distinctly different color patterns.

Conophis lineatus dunni Smith

Psammophis lineatus, Günther, Catalogue of Colubrine Snakes in the Collection of the British Museum, p. 135, 1858.

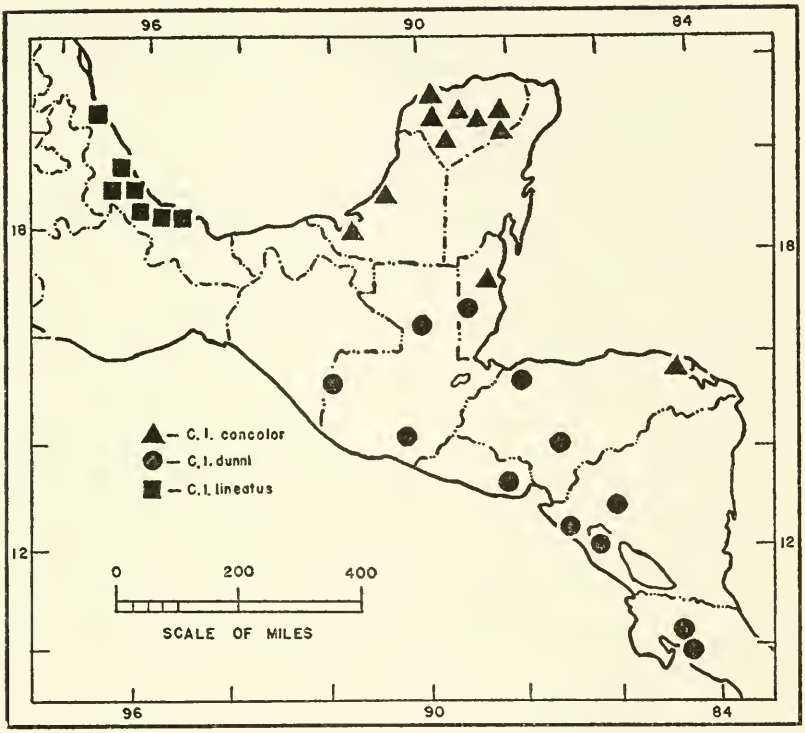


FIG. 2. Selected locality records for the subspecies of *Conophis lineatus*.

Conophis lineatus, Cope, 3rd Ann. Rept. Peabody Acad. Sci., p. 82, 1871; Proc. Acad. Nat. Sci. Philadelphia, 23:204, October 24, 1871; Journ. Acad. Nat. Sci. Philadelphia, ser. 2, 8:137, 1876; Bull. U. S. Natl. Mus., 32:77, 1887; Günther, Biologia Centrali-Americana, p. 165, March, 1895; Boulenger, Catalogue of the Snakes in the British Museum (Natural History), 3:122-123, 1896; Werner, Arch. Naturges., 90, abt. A, 12:143, 1925; Schmidt, Zool. Ser. Field Mus. Nat Hist., 12:199-200, November 21, 1928; Amaral, Mem. Inst. Butantan, 4:212, 1929; Werner, Zool. Jahrb., 57:184, 1929; Stuart, Occas. Papers Mus. Zool. Univ. Michigan, 292:5, June 29, 1934; Dunn, Copeia, no. 4:214, December 31, 1937.

Conophis lineatus similis Smith, Journ. Washington Acad. Sci., 31:123-124, March 15, 1941 (Type.—United States National Museum, No. 79963; type locality.—Managua, Nicaragua; *nec* Bocourt *in* Duméril, Bibron and Mocquard, Mission Scientifique au Mexique et dans l'Amerique Centrale, 2:647-648, 1886); Cochran, Bull. U. S. Natl. Mus., 220:167, 1961.

Conophis lineatus dunni Smith, Proc. U. S. Natl. Mus. 92:394-395, November 5, 1942; Savage, Trans. Kansas Acad. Sci., 50:483-486, December 31, 1949; Taylor, Univ. Kansas Sci. Bull., 34(pt. 1):145, October 1, 1951; Neill and Allen, Publ. Res. Div. Ross Allen's Rept. Inst., 2:56, November 10, 1959; Herpetologica, 16:146-148, fig. 2, September 23, 1960.

Conophis pulcher pulcher, Stuart, Misc. Publ. Mus. Zool. Univ. Michigan, 69:79, June 12, 1948; Contr. Lab. Vert. Biol. Univ. Michigan, 45:24,

May, 1950; Contr. Lab. Vert. Biol. Univ. Michigan, 49:14, August, 1951; Contr. Lab. Vert. Biol. Univ. Michigan, 65:19-20 (part), March, 1954.

Conophis pulcher plagosus, Mertens, Zool. Anz., 148:93, February, 1952; Abhand. Senken. Naturw. Gesell., 487:61-62, December 1, 1952.

Conophis lineatus nevermanni, Taylor, Univ. Kansas Sci. Bull., 37(pt. 1): 563-565, fig. 16, October 15, 1955.

Type.—United States National Museum, no. 79963, obtained by Lt. H. C. Kellers. Type locality: Managua, Nicaragua. There are also three paratypes; one a topotype (USNM 79964), one from "Nicaragua" (USNM 25237), and one from Esparta, Costa Rica (USNM 37758).

Diagnosis.—Lateral dark stripe anteriorly passing through eye and posteriorly involving 3rd and 4th scale-rows; 1st scale-row darkly pigmented; no paravertebral dark stripe, although vertebral row sometimes darkly pigmented; six to thirteen stripes at mid-body; eight supralabials immaculaate or having dark ventral margins.

Variation.—Thirty-six specimens have 159 to 178 (167.2±4.56) ventrals. Thirty of these snakes having complete tails have 60 to 80 (70.5±5.36) subcaudals; the number of ventrals plus subcaudals varies from 224 to 247 (237.6). In 36 specimens the reduction from 19 to 17 dorsal scales takes place between ventrals 91 and 111 (102.1 ± 4.59). Sexual dimorphism is evident in the number of subcaudals; 16 females have 60 to 72 (67.1), and 14 males have 67 to 80 (74.5) subcaudals. The largest specimen (ERA-WTN BH-300) is a female from Augustine, British Honduras, having a body length of 732 mm., a tail length of 183 mm. and a total length of 915 mm. A juvenile (MCZ 49794) from Tegucigalpa, Honduras, has a body length of 162 mm., a tail length of 51 mm. and a total length of 213 mm.

The greatest variation is in coloration. The ground-color is pale brown or white with dark stripes of black or deep brown present dorsally and laterally. Some specimens from Costa Rica have as many as 13 dark stripes at mid-body (fig. 1, C). In these snakes the first row of dorsal scales bears a series of large, slightly elongated, dark spots; on the 2nd row a narrow dark brown stripe on the middle of the scales; on the 3rd a black stripe on the dorsal one-third to one-half of the scales; on the 4th and the 7th rows black stripes on the medial half of the scales of each row; on the 8th and 10th (vertebral) rows dark brown stripes on the medial third of the scales of each row. A specimen from Guatemala (UMMZ 107339) shows the greatest reduction of stripes and dark pigmentation (fig. 1, A); it has only eight stripes at mid-body: on the first row of dorsal scales a discontinuous stripe is formed by a series of dashes; the 3rd row bears a series of small black spots near the base and tip of each scale; the 4th and 7th rows bear continuous black stripes on the medial third to fourth of the scales of each row; the 8th row has extremely small dark spots near the tips of some scales.

The primary stripes, chacteristic of the species *lineatus*, are those on the 1st, 4th and 7th rows of dorsal scales; these are the most prominent stripes. In some specimens these primary stripes begin as spots or dashes on the nape and become continuous stripes posteriorly; in others they are continuous for the length of the body. The stripe on the 1st row is most variable; usually it consists of only a discontinuous series of dashes for most of its length. The secondary stripes are those on the 3rd and 8th rows; of these, only the one on the 3rd scale-row is present on the nape. The stripe on the 3rd row in

combination with the dark stripe on the 4th row is the posterior continuation of the dark stripe that on the head passes through the eye; this stripe is characteristic of *C. lineatus dunni*. Both secondary stripes usually begin anteriorly as a series of spots or dashes and become continuous stripes posteriorly; occasionally near the base of the tail they fuse with the primary stripes on the 4th and 7th rows. In some specimens in Costa Rica indistinct stripes are present on the 10th (posteriorly the 9th) rows, and in some specimens in Honduras, Nicaragua, and Costa Rica similar indistinct stripes are present on the 2nd row.

Usually there are more or less conspicuous dark spots laterally on the ventrals, but in some specimens there are no spots. Except for the dark lateral spots (when present) the ventrals are immaculate white. The dorsal ground-color is a pale brown or brownish white in preserved specimens on the 1st, 2nd, 3rd and 4th rows of scales where dark stripes or spots are not present. The ground-color of the dorsum between the 5th rows on each side is a somewhat darker shade of pale to medium brown.

Never is more than the lower one-third of each of the supralabials brown. In many specimens little or no brown is present on the lower margins of these scales. Some of the specimens having brown on the supralabials also have dusky markings of tan or gray on the chin and infralabials. Specimens from the northern part of the range (Guatemala) less frequently have dark chins and supralabials than do specimens from the southern part of the range (Costa Rica). There is, nevertheless, at any one locality considerable variation in the amount of dark pigmentation present on the chin and supralabials, thereby indicating that the slight geographic trend in this character is not significant.

Probably the most common pattern of dorsal coloration consists of eight or ten dark stripes (fig. 1, B). In snakes having this pattern the stripes on the 1st, 3rd, 4th and 7th rows are always present and prominent, although those on the 1st and 3rd rows sometimes are present as discontinuous rows of dashes. The ground-color from the venter to the 7th row is usually pale brown, and that dorsally between the 7th rows on each side is usually a darker, medium brown. A series of spots or dashes or a continuous stripe is sometimes present on the 8th row of scales.

Snakes having a larger number of dark stripes and more dark pigmentation occur in the southern part of the range. There seems to be a cline from paler snakes having fewer stripes in the north to darker snakes in the south.

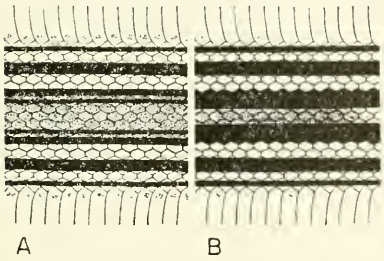


FIG. 3. Patterns of dorsal coloration at mid-body of juveniles of two sympatric species of *Conophis*. A. *C. lineatus dunni* (MCZ 49794) from Tegucigalpa, Honduras. B. *C. pulcher* (MCZ 49791) from Tegucigalpa, Honduras. Approximately × 1.

In juveniles, there are six or eight black stripes boldly contrasting with a white or pale tan ground-color (fig. 3, A). The first pair of stripes is on the

1st scale-row; the second pair, on the 3rd and 4th scale-rows; the third pair, on the 7th row; the fourth pair (when present), on the 8th row. Ontogenetic change in coloration consists of the splitting of the second pair of dark stripes in the juvenile. Additional stripes may form later on the 2nd and/or 10th rows of dorsal scales.

Remarks.—Savage (1949:483-486) stated that his specimen of *C. l. dunni* (from Honduras) resembled *l. lineatus* in having secondary stripes on the 2nd and 8th rows and dark pigmentation throughout the length of the 2nd row. As can be seen from the preceding discussion of variation, a specimen having this color pattern is clearly within the observed range of variation of *l. dunni.* The specimen in no way represents an intergrade between *C. l. dunni* and *l. lineatus.*

A specimen in the British Museum (Natural History), catalogued in 1853 (no. 53.2.4.16), has the locality listed as "México." Since this specimen is of *C. l. dunni* and this subspecies occurs only south of México, the locality must be considered erroneous; possibly the locality as recorded referred only to the fact that the specimen came from tropical Middle America.

The absence of paravertebral stripes, the presence of a lateral dark stripe on the nape involving the 3rd and 4th rows of scales, and the darkly pigmented 1st scale-row, in combination with the characteristics of the genus, distinguish *C. l. dunni* from all other snakes in México and Central America. The only sympatric species of this genus, *C. pulcher*, differs in that it has paravertebral stripes (though never a vertebral dark stripe). *Conophis pulcher* has a lateral dark stripe that includes the upper half of the second scale-row on the anterior part of the body; stripes of *C. l. dunni* never include more than the 3rd and 4th rows. Even as juveniles the paravertebral row is not darkly pigmented in *C. l. dunni* as it is in *C. pulcher.*

Distribution.—Semi-arid habitats from sea level to elevatons of 1000 m. from the Cuilco Valley in western Guatemala, El Peten and British Honduras southeastward to northeastern and southern Honduras, western Nicaragua and northwestern Costa Rica (fig. 2).

Specimens examined.—Total of 41 specimens, as follows: BRITISH HONDURAS: *Cayo District*: Augustine, ERA-WTN BH-300; *Mountain Pine Ridge, 10 mi. E Augustine,* ERA-WTN BH-298.

COSTA RICA: *no specific locality,* AMNH 17309. *"Cartago,"* BMNH 71.11.22.15. *Puntarenas:* 32 km. N Barranca, KU 35630; Esparta, USNM 37758. *"San José,"* ANSP 3480, 12232.

EL SALVADOR: *Morazan:* El Divisadero, CNHM 10999. *San Miguel: San Pedro,* MCZ 57061.

GUATEMALA: *El Petén:* Sojio (Toocog), AMNH 69969, 69986. *Huehuetenango:* flood plain Río Cuilco, W of Finca Canibal, 18 km. N Tacaná, UMMZ 98283. *Santa Rosa:* Santa Rosa, UMMZ 107339.

HONDURAS: *no specific locality,* AMNH 32814, UF 7657. *Cortes: Cofradía,* SU 8422; *Gracias,* CNHM 28560; *Hacienda de Santa Ana, W San Pedro Sula,* CNHM 5297; San Pedro Sula, UMMZ 68695(2); *near San Pedro Sula,* MCZ 27563. *Francisco Morazan: Potrero de Melio, Escuela Agricola Panamericana,* MCZ 49987; Tegucigalpa, MCZ 49784, 49786, 49789-90, 49792, 49794.

MEXICO: *no specific locality,* BMNH 53.2.4.16.

NICARAGUA: *no specific locality,* UMMZ 65633, USNM 25237. *Leon:* El *Polvón,* MCZ 5645, 5696. *Managua:* Managua, USNM 79963-64; *3 mi. SW Managua,* KU 42315; *8 mi. WNW Managua,* KU 42314; *1 mi. N Sabana Grande,* KU 42311-13. *Matagalpa:* 1.5 mi. N Matagalpa, UMMZ 116537.

Conophis lineatus lineatus (Dumeril, Bibron and Dumeril)

Tomodon lineatum (in part) Duméril, Bibron and Duméril, Érpétologie Générale, 7(pt. 2):936-938, atlas, pl. 73, February 25, 1854; Bocourt, Journ. de Zool., 5:406-407, 1876.

Tomodon lineatus, Jan, Arch. Zool. Anat. Fis., Genoa, 2(2):234, March 1863; Elenco sistematico degli ofidi. Milano, p. 57, 1863; Muller, Reisen in den Vereinigten Staaten, Canada, und Mexico. Bd. 3. Beitrage zur Geschichte, Statistik, und Zoologie von Mexiko. 3:607, 1865; Jan and Sordelli, Iconographie Generale des Ophidiens, Milano. liv. 19, pl. 6, fig. 3, December, 1866; liv. 50, pl. 2, fig. 34, November, 1881.

Tachymenis lineata (in part), Garman, Bull. Essex Inst., 16: 33, January 9, 1884; Mem. Mus. Comp. Zool., 8:60-61, July, 1884.

Conophis lineatus, Bocourt *in* Duméril, Bocourt and Mocquard, Mission Scientifique au Mexique et dans l'Amerique Centrale, 2:643-644, pl. 38, fig. 5, 1886; Cope, Trans. Amer. Philos. Soc., 18:218, pl. 28, fig. 2, (hemipenis), April 15, 1895; Boulenger, Catalogue of the Snakes in the British Museum (Natural History), 3:122-123 (part), 1896; Cope, Ann. Rept. U. S. Natl. Mus. for 1898, pp. 1094-1095, 1242, pl. 26, fig. 2, (hemipenis), 1900; Amaral, Mem. Inst. Butantan, 4:212, 1929; Mittleman, Copeia, no. 2:122, June 30, 1944.

Conophis lineatus lineatus, Smith, Journ. Washington Acad. Sci., 31:122, March 15, 1941; Proc. U. S. Natl. Mus., 92:395, November 5, 1942; Proc. U. S. Natl. Mus., 93:407, October 29, 1943; Smith and Taylor, Bull. U. S. Natl. Mus., 187:43, October 5, 1945; Shannon and Smith, Trans. Kansas Acad. Sci., 52:505, December 31, 1949; Smith and Taylor, Univ. Kansas Sci. Bull., 33(pt. 2):351, March 20, 1950; Werler and Smith, Texas Journ. Sci. 4(4):565, December 30, 1952; Fugler and Dixon, Herpetologica, 14:186, December 1, 1958.

Type.—Museum National d'Histoire Naturelle, Paris, no. 3738. Type locality.—"México," restricted to Veracruz, Veracruz, México, by Smith and Taylor (1950:351). Little is known about the type specimen, and nothing, concerning its collector or the locality at which it was collected. Smith (1941:122) assumed that the specimen illustrated by Bocourt in Duméril, Bocourt, and Mocquard (1886:pl. 38, fig. 5) was the type of *C. l. lineatus.* I have also made this assumption concerning the identity of the type specimen of this species, especially because of the many inconsistencies appearing in the plate accompanying the description by Duméril, Bibron and Duméril (1854:pl. 73), and by Jan and Sordelli (1866:pl. 6). Neither show the nape nor a regular number of dorsal scales by which accurate determination of color pattern can be made and by means of which *C. l. dunni* and *C. l. lineatus* can be separated.

Diagnosis.—Lateral dark stripe anteriorly passing through eye and posteriorly involving fourth scale-row only; first scale-row darkly pigmented; no

paravertebral stripe; no dark pigment on vertebral row; six or eight dark stripes at midbody, secondary stripes often present posteriorly; usually eight (sometimes seven) supralabials immaculate or having dark ventral margins.

Variation.—Twenty-six specimens have 157 to 169 (163.5 ± 3.59) ventrals. Twenty of these snakes having complete tails have 60 to 73 (66.5 ± 4.26) subcaudals; the number of ventrals plus subcaudals varies from 224 to 238 (230.1) in nineteen of these. In 26 specimens the reduction from 19 to 17 dorsal scale-rows takes place between ventrals 91 and 107 (100.2 ± 3.59). Sexual dimorphism is evident in the number of subcaudals; nine females have 60 to 66 (62.4), and 11 males have 68 to 73 (69.8) subcaudals. The largest specimen (AMNH 19643) is a male from "México," having a body length of 626 mm., a tail length of 168 mm. and a total length of 786 mm. No small juveniles have been examined; the smallest specimen (AMNH 19618) is a male from Veracruz, México, having a body length of 325 mm., a tail length of 90 mm. and a total length of 415 mm.

The greatest variation is in coloration. In preserved specimens the ground-color is white, tannish-white, or often pale blue, with dark stripes of black or deep brown present dorsolaterally and laterally. Secondary stripes of paler brown are sometimes present, but the pale browns have faded badly on many specimens. Normally four black stripes are present at midbody—a lateral pair on the 4th row of dorsal scales and a dorsolateral pair on the 7th row (fig. 1, D). The lateral pair is the posterior continuation of the stripe that on the head passes through the eye; it continues on the nape as a narrow stripe on the 4th row only. In a few specimens the lateral stripe broadens to include the upper third of the 3rd row posterior to the nape. In some specimens both the dorsolateral and lateral dark stripes are present on the nape as a row of elongated spots or dashes that become continuous stripes of even width one-third to one-half of the distance posteriorly along the body; in other specimens the stripes are continuous on the nape. Posterior to the place of dorsal scale-reduction from 19 to 17 rows by the fusion of the 3rd and 4th rows, the lateral and dorsolateral stripes are moved downward by one row. In some specimens secondary black or dark brown stripes are present in the form of a series of dashes on the 5th and 8th rows; posterior to the place of scale reduction, these dashes are on the 4th and 7th rows. These dashes form a continuous stripe near the base of the tail. On the tail the secondary and primary stripes on adjacent rows sometimes fuse into a single broader stripe.

Usually the 1st row of dorsal scales is dark brown; in some specimens the brown on the 1st or 7th row has faded in preservative. A few specimens have small black spots on the moderate brown background of the 1st row; in others the 1st row is only a somewhat darker brown than the ground-color. The 2nd row sometimes is a medium brown, and appears to be an additional stripe.

The ventrals usually have more or less conspicuous dark spots laterally; in some specimens there are no spots. Except for the lateral spots (when present) the ventrals are immaculate white. The dorsal ground-color is pale brownish-white, white or pale blue between the 4th and 7th rows of dorsal scales and dorsally between the 7th rows on each side. Stripes are never present on the uniformly pale colored 8th, 9th and vertebral scale-rows.

Usually there are eight supralabials on each side; however, seven of the 27 specimens examined have seven supralabials on each side, and three others

have seven on one side, and eight on the other. Never is more than the lower third of the supralabials dark brown. In many specimens little or no brown is on the supralabials. There is little or no brown on the chin.

Variation in coloration and in number of supralabials appears to be of no geographic significance.

Although no juveniles have been collected, I expect that juveniles resemble adults in coloration. Probably there would be a greater contrast between the dark stripes and the pale ground-color in juveniles.

In life an adult from three miles northwest of Lerdo de Tejada, Veracruz, México (UMMZ 114484), had black stripes on the 4th and 7th rows of dorsal scales, and black spots on a brown background on the 1st row. The 2nd row had a medial, pale to medium brown auxiliary stripe on a brownish-white background. Posterior to the nape the 3rd row was medium brown. The area between the 4th and 7th rows and the dorsum between the 7th row of scales on each side was a pale brownish-white. Posterior to the place of scale-reduction the primary stripes were displaced downward by one row to the 3rd and 6th rows and secondary stripes originated as elongated spots on the 4th and 7th rows. Near the tail the secondary stripes were broad and continuous. The head was white or tannish-white with three dark brown or black stripes.

Remarks.—In his diagnosis of *C. l. lineatus,* Smith (1941:122) states: "lateral dark stripe . . . very narrow posterior to nape, extending along fourth scale row; posteriorly a stripe along third and eighth (farther posteriorly the seventh) scale rows; a narrow dark stripe along sixth scale row, continuous throughout length of body . . ." I fail to find a dark stripe on the 6th row throughout the length of the body. In all specimens that I have seen, there is a dark stripe on the 7th row anteriorly and on the 6th row posteriorly. In many specimens the stripes on the 3rd and 8th (posteriorly the 7th) scale-rows are absent or present so far posteriorly that the 8th row is never involved.

The dark brown on the first scale-row and the presence of a lateral dark stripe on the 4th row of dorsal scales only, in combination with the characteristics of the genus, distinguish *C. l. lineatus* from all other snakes in México.

Distribution.—Semi-arid habitats on the coastal plain of Veracruz, México, from Tecolutla to Lerdo de Tejada and Piedras Negras (fig. 2).

Specimens examined.—Total of 27, as follows: MÉXICO: *no specific locality,* AMNH 19614-15, 19621-24, 19642-43, NMW 16827. *Veracruz: no specific locality,* AMNH 19618-20, CAS 73640, NMW 16829; *4 km. S Alvarado,* KU 58124; *14 mi. N Alvarado,* UIMNH 46978; 6 mi. SE Boca del Río, UIMNH 28023; Etiopa, 2 mi. S Tecolutla, UIMNH 3847; *ca.* 30 mi. E Jalapa, AMNH 81948; 3 mi. NW Lerdo de Tejada, UMMZ 114484-85; Paso del Macho, USNM 109708; Río Blanco, 20 km. WNW Piedras Negras, KU 23253; Veracruz, AMNH 19612, UF 8990; *W side Veracruz,* AMNH 19616; *2 mi. W Veracruz,* AMNH 19617, 19619.

Conophis lineatus concolor Cope

Conophis vittatus Cope, Proc. Acad. Nat. Sci. Philadelphia, 13:300, December 28, 1861 (*nec* Peters, 1860; type.—United States National Museum, no. 4941; type locality—"Petén," Guatemala); Journ. Acad. Nat. Sci. Philadelphia, ser. 2, 8:137, 1876; Bull. U. S. Natl. Mus., 32:76, 1887.

Conophis concolor Cope, Proc. Acad. Nat. Sci. Philadelphia, 18:318-319, February 20, 1867; Journ. Acad. Nat. Sci. Philadelphia, ser. 2, 8:137, 1876; Bocourt *in* Duméril, Bocourt and Mocquard, Mission Scientifique au Mexique et dans l'Amerique Centrale, 2:648, 1886; Müller, Verh. Ges. Basel, 8:263, 1887; Cope, Bull. U. S. Natl. Mus., 32:77; 1887; Ann. Rept. U. S. Natl. Mus. for 1898, p. 1095, 1900; Schmidt and Andrews, Zool Ser. Field Mus. Nat. Hist., 20:178, October 31, 1936; Andrews, Zool. Ser. Field Mus. Nat. Hist., 20:358, December 28, 1937; Smith, Occas. Papers Mus. Zool. Univ. Michigan, 388:7, October 31, 1938; Taylor and Smith, Univ. Kansas Sci. Bull., 25:253, July 10, 1939; Smith, Zool. Ser. Field Mus. Nat. Hist., 24:31, January 30, 1939; Cochran, Bull. U. S. Natl. Mus., 220:167, 1961; Neill and Allen, Herpetologica, 17:44-46, fig. 3, April 15, 1961.

Conophis lineatus (in part), Günther, Biologica Centrali-Americana, p. 165, March, 1895; Gaige *in* Pearse, *et al.* Carnegie Inst. Washington Publ., 457:302, February 5, 1936.

Conophis lineaticeps Cope, Ann. Rept. U. S. Natl. Mus. for 1898, pp. 1094-95, 1900 (Substitute name for *Conophis vittatus* Cope, 1861, *nec* Peters, 1860).

Conophis lineatus concolor, Smith, Journ. Washington Acad. Sci., 31:122-123, March 15, 1941; Proc. U. S. Natl. Mus., 92:395, November 5, 1942; Proc. U. S. Natl. Mus., 93:407, October 29, 1943; Smith and Taylor, Bull. U. S. Natl. Mus., 187:43, October 5, 1945; Univ. Kansas Sci. Bull., 33(pt. 2):352, March 20, 1950.

Types.—Two in the United States National Museum, no. 12368 (two specimens). Type locality: "Yucatán," restricted to Chichén Itzá, Yucatán, México by Smith and Taylor (1950:352).

Diagnosis.—Dark stripes either absent posterior to the nape, or present as a row of small spots on fourth or seventh scale-row; no dark stripe on first scale-row; eight supralabials having dark ventral margins.

Variation.—Forty-five specimens have 158 to 170 (163.7 ± 1.56) ventrals. Thirty-eight of these snakes having complete tails have 56 to 74 (66.7 ± 4.77) subcaudals; the number of ventrals plus subcaudals varies from 222 to 245 (230.6). In 45 specimens the reduction from 19 to 17 dorsal scales takes place between ventrals 89 and 114 (102.5 ± 5.57). Sexual dimorphism is evident in the number of subcaudals; 16 females have 56 to 65 (61.8), and 22 males have 68 to 74 (70.3) subcaudals. The longest specimen (USNM 46395) is a male from Chichén Itzá, Yucatán, having a body length of 893 mm., a tail length of 274 mm., and a total length of 1167 mm. A juvenile (AMNH 38833) from Chichén Itzá, Yucatán, has a body length of 194 mm., a tail length of 50 mm., and a total length of 244 mm.

The venter is immaculate white or pale yellow and the dorsum of the body is immaculate pale gray to pale olive. Some specimens have small dark brown spots on the tips of the scales of the 4th or of the 7th row, but never on both. Only on the nape are spots present on both the 4th and the 7th rows; these spots are the posterior continuations of the dark stripes on the head and on many specimens do not reach the nape. Posterior to the place of scale reduction from 19 to 17 rows by the fusion of the 3rd and 4th rows of scales, the dark spots (when present) are on the 3rd or 6th row of scales.

The coloration of juveniles is the same as that of adults. Color in life is thought not too different from that of preserved specimens, for notes on the color of living individuals (Neill and Allen, 1961:44) agree with what I have observed on preserved snakes.

Remarks.—The specimen from "Petén" (USNM, no. 4941) is the only specimen that has a controversial history. As can be seen from the synonymy of the species, the relationship of this specimen with the rest of the genus has been interpreted in several ways. Smith (1941:122-123) stated that the above specimen was catalogued as being from El Salvador; however, the locality was presumed by him to be El Petén, Guatemala, due to the presence in the bottle of a piece of paper inscribed *"Conophis vittatus,* Petén, J. M. Dow." This specimen is the one mentioned by Cope (1861:300, 1876:76, and 1900:1094-95), and in the first paper is ascribed to Guatemala. In 1900 this specimen was named *C. lineaticeps* by Cope who thought the specimen differed significantly from *C. concolor* (Cope, 1867:318-319). This specimen has the coloration normal for *C. l. concolor* as far posteriorly as mid-body; beyond mid-body the dark lines, typical of *C. l. lineatus* or of *C. l. dunni,* are present. It is likely that this specimen is an intergrade between *C. l. concolor* and *C. l. dunni,* the other subspecies present in Guatemala.

The only specimen not from the Yucatán Peninsula is allegedly from Patuca, Honduras (USNM 20271). It was obtained in the 1870's. Possibly more collecting will verify the presence of *C. l. concolor* in northern Honduras. This individual may be merely a genetically aberrant specimen from an area where normal specimens are *C. l. dunni.* Neill and Allen (1961:44-45) suggested that the specimen from Patuca implies widely overlapping distributions for *C. l. dunni* and *C. concolor.* The occurrence of *C. l. concolor* in Honduras needs to be verified before this assumption is made. There can, therefore, at present be no objection to the view that intergradation between the subspecies *C. l. dunni* and *C. l. concolor* could occur through a relatively broad area of El Petén and British Honduras.

Neill and Allen (1961:44-45) further suggest that the present range of *C. l. dunni* extends "presumably still farther northward toward the Méxican state of Veracruz where *C. l. lineatus* exists." Actually the presence of the subspecies *C. l. dunni* and *C. l. lineatus* as presently disjunct populations implies merely that they were presumably a continuous population at some time in the past.

The characteristics of the genus in combination with the reduc-

tion of dark coloration posterior to the head distinguish this snake from all other snakes in México and Central America.

Distribution.—The Yucatán Peninsula: eastern Campeche, all of Yucatán, probably in Quintana Roo, and the northern third of British Honduras. A record for northeastern Honduras is questioned (fig. 2).

Specimens examined.—Total of 48, as follows: BRITISH HONDURAS: *Belize District:* 13.0 mi. W, 1.5 mi. S Belize, ERA-WTN BH-1562.

GUATEMALA: *El Petén, no specific locality,* USNM 4941.

HONDURAS: *Colón:* Patuca, USNM 20271.

MEXICO: *Campeche:* Champotón, UMMZ 73063-66; Encarnación, CNHM 106462. *Yucatán: no specific locality,* BMNH 80.7.13.30; Chichén Itzá, AMNH 38826, 38833, CNHM 20610-11, 26986-87, 36299-300, 36303-04, 36307, 36316, MCZ 7422, 28748, UMMZ 68236, 73060-62, 80806, USNM 46395; Kantunil, CNHM 36301, 36305-06, 36308-09, 36312-13; *Libré Union,* CNHM 36298, 36302, 36310-11, 36314; Mayapán, CNHM 40720; Mérida, CNHM 19411, 19413, NMW 16828; Progreso, CNHM 40721; Tekom, CNHM 49374; Yokdzonot, CNHM 36315.

Conophis nevermanni Dunn

Coniophanes imperialis imperialis, Wettstein, Sitz. Akad. Wiss. Wien. mathem-naturw. Kl., 143:37-38, 1934.

Conophis nevermanni Dunn, Copeia, no. 4:214, December 31, 1937; Smith, Proc. U. S. Natl. Mus., 92:395, November 5, 1942; Savage, Trans. Kansas Acad. Sci., 50:484, December 31, 1949; Taylor, Univ. Kansas Sci. Bull., 34(pt. 1):145-146, October 1, 1951.

Type.—Academy of Natural Sciences of Philadelphia, no. 22423, obtained by Emmet R. Dunn from Prof. Manuel Valerio. Type locality: Río Poas de Aserri (a few miles south of San José), Costa Rica.

Diagnosis.—Head and body dark brown or black above with two or four white stripes along body; usually two white lines on head immediately above eye passing from canthus rosetralis posteriorly to connect with white stripe on 6th row of dorsal scales; eight supralabials with black margins above.

Variation.—Six specimens have 173 to 183 (176.5 ± 4.00) ventrals. Five of these snakes having complete tails have 71 to 89 (80.6 ± 7.15) subcaudals; the number of ventrals plus subcaudals varies from 250 to 263 (257.0). In the six specimens the reduction from 19 to 17 dorsal scales takes place between ventrals 84 and 97 (93.2 ± 4.71). Sexual dimorphism is evident in the number of subcaudals; two females have 71 and 76 (73.5), and three males have 82 to 89 (85.3) subcaudals. The longest specimen (ANSP 22424) is a female from San José, Costa Rica, having a body length of 660 mm., a tail length of 168 mm. and a total length of 828 mm.

The dorsal coloration (fig. 1, E) varies from a black ground-color with two or four narrow white stripes to a dark brown ground-color with a series of black stripes and four white stripes. In the black specimens there are no dark stripes. The darkest specimen (NMW 16838:1) has only two white stripes; these more or less continuous stripes are on the ventral third of the 2nd row of scales and occasionally on the dorsalmost part of the first scale-row. The venter is immaculate white except for black on the tips of the ventral scales. The dorsum above the 2nd scale-row is uniform black. There are no white stripes on the head.

The palest specimen (NMW 16838:2) has four dorsal white stripes; the lateral pair of these stripes is on the ventral half of the 2nd and the dorsal third of the 1st scale-rows; the dorsolateral pair is on the dorsal two-thirds of the 6th and the ventral third of the 7th rows of scales. This latter stripe is the posterior continuation of the white stripe on the head, which originates immediately posterior to the rostral scale and passes posteriorly along the canthus rostralis and along the lateral margin of the supraocular scale to the nape. Posterior to the place of scale reduction, the dorsolateral white stripe is displaced ventrally one scale-row. Except for black flecks or spots on the lateral margins of the ventrals, the venter is immaculate white. The dorsum above the lateral white stripes is brown and black; there is a pair of dorsolateral white stripes. The dorsal half of the 2nd, most of the 3rd, 4th and 5th rows of scales are black; the dorsal margin of the 3rd, both margins of the 4th, and the ventral margin of the 5th rows are paler brown. The dorsal two-thirds of the 7th, all but the dorsal most part of the 8th, and the middle two-thirds of the 10th scale-rows are black; the areas between are a medium brown.

Only six specimens are available on which to base a description of the variation in this species. Furthermore, there are no juveniles, notes on the colors of living individuals, or photographs of this species.

Remarks.—Taylor (1955:563-565) hesitantly referred a specimen (KU 35630) from 32 kilometers north of Barranca, Puntarenas

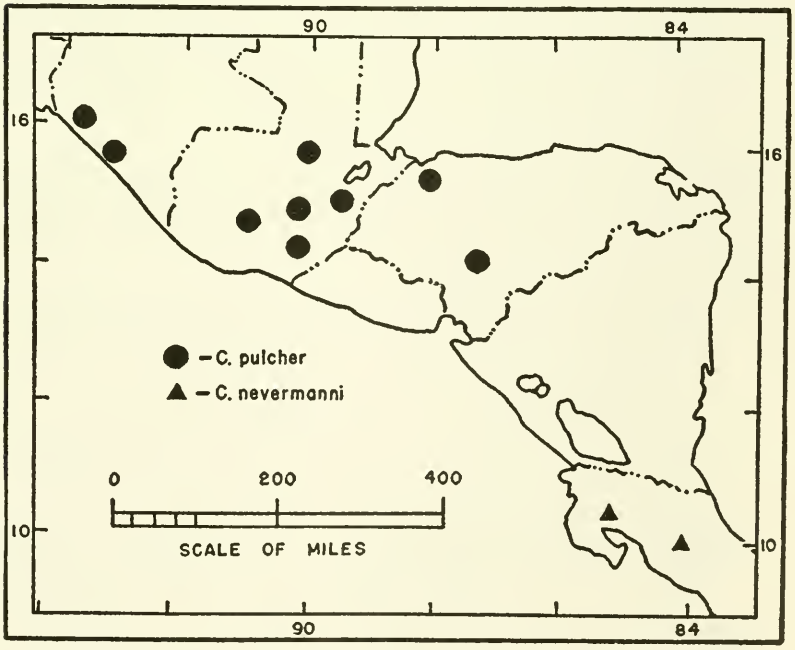


FIG. 4. Selected locality records for *Conophis pulcher* and *Conophis nevermanni.*

Province, Costa Rica, to *Conophis lineatus nevermanni.* This specimen, a female, has 169 ventrals and ventral scale-reduction taking place opposite the 109th ventral; both of these characters are well out of the range of *C. nevermanni.* Furthermore, the ventral margins of the supralabials are brown, and the pale dorsal stripes are tan and too wide for *C. nevermanni* (compare figs. 1, C and E). The specimen definitely is *C. lineatus dunni,* and corresponds well with another specimen from Costa Rica (ANSP 12232).

The dark brown or black dorsum with two or four white stripes and the presence of eight supralabials having dark brown dorsal margins, in combination with the characters of the genus, serve to distinguish *Conophis nevermanni* from other Central American snakes.

Distribution.—Pacific coastal plain of northwestern Costa Rica and the Meseta Central of central Costa Rica (fig. 4).

Specimens examined.—Total of six, as follows: COSTA RICA: *Guanacaste:* Bebedero, Río Tenorio, NMW 16838(5). *"San José,"* ANSP 22424.

Conophis pulcher Cope

Tomodon lineatus (in part), Salvin, Proc. Zool. Soc. London, 28:455, 1860.

Conophis pulcher Cope, Proc. Acad. Nat. Sci. Philadelphia, 20(5):308, 1869; Journ. Acad. Nat. Sci. Philadelphia, ser. 2, 8:137, 1876; Bocourt *in* Duméril, Bocourt and Mocquard, Mission Scientifique au Mexique et dans l'Amerique Centrale, 2:646-648, pl. 38, fig. 6, 1886; Ferrai-Perez, Proc. U. S. Natl. Mus., p. 196, September 28, 1886; Cope, Bull. U. S. Natl. Mus., 32:77, 1887; Trans. Amer. Philos. Soc., 18:194, April 15, 1895; Ann. Rept. U. S. Natl. Mus. for 1898, p. 1095, 1900; Alvarez del Toro, Reptiles de Chiapas, pp. 154-155, 1960.

Tomodon pulcher, Bocourt, Journ. de Zool., p. 408, 1876.

Conophis pulcher var. *similis* Bocourt *in* Duméril, Bocourt and Mocquard, Mission Scientifique au Mexique et dans l'Amerique Centrale, 2:647-648, pl. 38, fig. 6, 1886 [Type.—Museum National d'Histoire Naturelle, Paris, no. 6090; type locality.—unknown, restricted to Tonalá, Chiapas, by Smith and Taylor (1950:326)].

Conophis lineatus, Günther, Biologia Centrali-Americana, p. 165, March, 1895; Boulenger, Catalogue of the Snakes in the British Museum (Natural History), 3:122-123, 1896; Stuart, Occas. Papers Mus. Zool. Univ. Michigan, 292:5, June 29, 1934; Slevin, Proc. California Acad. Sci. 4th Ser., 23:409, December 29, 1939.

Conophis pulcher pulcher, Smith, Journ. Washington Acad. Sci., 31:121, March 15, 1941; Proc. U. S. Natl. Mus., 92:395, November 5, 1942; Stuart, Contr. Lab. Vert. Biol. Univ. Michigan, 65:19-20 (part), March, 1954; Contr. Lab. Vert. Biol. Univ. Michigan, 68:63, November, 1954; Cochran, Bull. U. S. Natl. Mus., 220:167, 1961.

Conophis pulcher plagosus Smith, Journ. Washington Acad. Sci. 31:121-122, March 15, 1941 (Type.—United States National Museum, no. 109707; type locality: Tonalá, Chiapas); Smith and Taylor, Univ. Kansas Sci. Bull., 33(pt. 2):326, March 20, 1950; Stuart, Contr. Lab. Vert. Biol. Univ. Michigan, 65:19-20, March, 1954; Cochran, Bull. U. S. Natl. Mus., 220:167, 1961.

Conophis pulcher similis, Smith, Proc. U. S. Natl. Mus., 92:395, November 5, 1942; Proc. U. S. Natl. Mus., 93:408, October 29, 1943; Smith and Taylor, Bull. U. S. Natl. Mus., 187:43-44, October 5, 1945; Univ.

Kansas Sci. Bull., 33(pt. 2):43-44, March 20, 1950; Maldonado-Koerdell, Inst. Mexicanos Recursos Nat. Renov. pp. 132-133, 1953.

Types.—Three in the United States National Museum, nos. 6751 (2 specimens) and 6803, obtained by Henery Hague. Type locality: "Petén," or "Verapaz," Guatemala. There is much doubt about localities for many of Hague's specimens collected in the 1860's (Stuart, 1948:10). Since *Conophis pulcher* is found predominantly in semi-arid environments, the types might have come from the semi-arid Cahabón, Negro, or Salamá river basins—all places near the sugar plantation that Hague managed at San Jerónimo, Baja Verapaz. Possibly the types were obtained from as far away as the Motagua Valley or the southeastern highlands of Guatemala, both of which areas Hague is known to have visited.

Diagnosis.—Paravertebral stripes present at least posteriorly (fig. 1, F); eight or ten stripes at mid-body; lateral dark stripe passing through eye anteriorly and including at least upper one-half of second scale-row from neck region posteriorly to place of scale reduction near mid-body; eight supralabials immaculate or having dark ventral margins.

Variation.—Twenty-six specimens have 161 to 182 (169.5±5.31) ventrals. Eighteen of these snakes with complete tails have 65 to 79 (70.6±3.93) subcaudals; the number of ventrals plus subcaudals varies from 231 to 251 (239.3). In 26 specimens the reduction from 19 to 17 dorsal scales takes place between ventrals 94 and 119 (104.6 ± 4.90). Sexual dimorphism is evident in the number of subcaudals; eleven females have 65 to 71 (68.2), and seven males have 70 to 79 (74.3) subcaudals. The longest specimen (AMNH 58364) is a female from El Zamarano, Honduras, having a body length of 703 mm., a tail length of 164 mm. and a total length of 867 mm. The smallest juvenile (MCZ 49793) from Tegucigalpa, Honduras, has a body length of 162 mm., a tail length of 46 mm. and a total length of 208 mm.

The dorsal ground-color is pale brown or white; black or dark brown stripes are present dorsally and laterally. Normally ten stripes are present at mid-body; the first pair on the first row of dorsal scales; the second pair on the upper half of 2nd and lower part of 3rd rows; the third pair on 4th row; the fourth pair on 7th and sometimes part of 8th rows; the fifth pair (paravertebral stripes) on the 9th row. Posterior to the place of reduction from 19 to 17 rows by the fusion of the 3rd and 4th rows, the third, fourth and fifth pairs of stripes are displaced downward one row. Sometimes the second and third pairs of stripes are fused resulting in only eight stripes at mid-body. On some specimens the fourth and fifth pairs of stripes are close together, but in none are they fused so as to result in a pattern of six stripes at mid-body.

The paravertebral stripes begin anteriorly on the nape or at any point on the anterior one-third of the body and continue as discrete stripes onto the base of the tail. Anteriorly these stripes are always broken into a series of dashes; posteriorly the stripes are continuous. In specimens in which the paravertebral stripes do not begin on the anterior-most part of the body, there is no paravertebral pigmentation anteriorly.

In addition to the paravertebrals, the other dorsal dark stripes are variable. In some specimens the stripes are present anteriorly and gradually disappear near mid-body (the first dark stripe only on three specimens). In other

specimens the stripes are present anteriorly as dashes and become continuous at mid-body; in others the stripes are continuous throughout. Posteriorly continuous stripes are of uniform width; anteriorly sometimes they are wide on the tip of each scale and narrow on the base (fig. 1, F). The variation in continuity and width described above is found in all of the dorsal dark stripes.

The ventrals usually have more or less conspicuous dark spots laterally; in some specimens there are no spots. Except for the dark lateral spots, when present, the ventrals are immaculate white. Usually the dorsal ground-color is a pale tan, especially between the first and second, and the third and fourth dark stripes. The areas between the second and third dark stripes and across the dorsum between the fourth stripes on each side are pale brown. In some specimens the dorsum between the paravertebral stripes is still paler brown.

Never is more than the lower third of the supralabials brown. Many specimens have little brown, and others none. In most of those specimens having brown on the supralabials, the chin and infralabials are dusky tan or gray. There is little or no brown on the supralabials or the chin in the northern part of the range (Chiapas), whereas the greatest amount of brown on the labials and chin is found on some specimens from the southern part of the range (Honduras). Since there is considerable variation in the amount of brown on the chin and labials of specimens from single localities, the slight geographic trend in this character seemingly is not significant.

In juveniles six black or dark brown stripes boldly contrast with a white or pale tan ground-color. At mid-body the first pair of dark stripes is on the 1st scale row; the second pair on the 3rd and 4th rows; the third pair on the 7th, 8th and at least the lower half of the 9th rows (fig. 3 B). Ontogenetic change in coloration consists of the splitting of the second and third pairs of dark stripes in the juvenile. The first stripe does not split. Consequently adults have ten dark stripes.

In life an adult from Tonalá, Chiapas, had black stripes. The ground-color below the second stripe, and between the third and fourth dark stripes was tan. The area between the second and third dark stripes was reddish-brown, as was the dorsum between the fourth pair of dark stripes, except that the 10th scale-row was paler.

Three excellent photographs of this species have been published under the name *Conophis lineatus* (Ditmars, 1931:pls. 26 and 27).

Remarks.—Smith (1941:121-122) described *C. pulcher plagosus* from Tonalá, Chiapas, and characterized the subspecies by its having "(1) the ventrals completely unspotted; (2) secondary lines on paravertebral rows not continuous posteriorly; (3) all other lines on body also somewhat spotted in appearance; (4) dusky markings on chin and supralabial border very dim (less distinct than in *p. pulcher* or any member of the *lineatus* series)." Although all Chiapan specimens lack ventral spots, specimens from Guatemala have no spots, small spots, or large spots. Even in specimens from Tegucigalpa, Honduras, the southernmost limit of the range, the spotting varies from a few inconspicuous spots to many large

spots. Paravertebral rows were continuous posteriorly in all specimens examined by me. Likewise, all other stripes were continuous bands of uniform width posteriorly, having appeared anteriorly as rows of spots or dashes. The amount of brown on the chin and labials has been shown previously not to be geographically significant. The absence of characters of adequate significance to separate populations precludes the naming of subspecies in this species.

Mertens (1952a:93, and 1952b:61-62) designated three specimens from El Salvador as *C. pulcher plagosus.* In the latter paper, Mertens, on the basis of a description of a specimen of "*C. lineatus*" from Divisadero, El Salvador, given by Schmidt (1928:200), referred that specimen also to *C. pulcher plagosus.* I have examined this specimen and refer it to *C. lineatus dunni.* Although I have not seen Merten's specimens, on the basis of the excellent descriptions given by Mertens (1952b:61-62), I refer the three Salvadoranean specimens to *C. lineatus dunni.*

The presence of paravertebral stripes in combination with the characteristics of the genus distinguish *Conophis pulcher* from all other snakes in southern México and Central America. The only sympatric species of this genus, *C. lineatus dunni,* differs in that it lacks paravertebral stripes, although it may have a single vertebral stripe. *Conophis lineatus dunni* has lateral dark stripes that are present on the 3rd and 4th scale-rows, never on the anterior third of the body as in *C. pulcher.* Even in juveniles the third pair of dark stripes includes the lower part of the 9th scale-row in *C. pulcher,* whereas the dorsal most dark stripe of *C. lineatus dunni* never includes more than the lower part of the 8th scale-row.

Distribution.—Pacific coastal region of Chiapas, México, southeastward into Guatemala; southeastern highlands and the dry valley of central and eastern Guatemala; Caribbean lowlands of Honduras southward to the region of Tegucigalpa, Honduras (fig. 4).

Specimens examined.—Total of 27, as follows: GUATEMALA: *no specific locality,* CNHM 22912, NMW 16830. *Jutiapa:* Hacienda Mongoy, UMMZ 106725. *El Progreso:* El Progreso, CAS 67000; *El Rancho,* UMMZ 106724; *San Antonio,* CAS 66999. "Peten," USNM 6751(2), 6803. *Sacatepequez:* Dueñas, BMNH 64.1.26.17, 64.1.26.126-127. *Zacapa:* Pepesca, AMNH 72555-56.

HONDURAS: *no specific locality,* AMNH 58364. *Cortes:* San Pedro Sula, CNHM 5295-96. *Francisco Morazan: El Zamarano,* AMNH 70189; Tegucigalpa, MCZ 49785, 49787-88, 49791, 49793, 49795.

MEXICO: *Chiapas:* Soconusco, UIMNH 33646-47; Tonalá, USNM 109707.

Conophis vittatus Peters

Tomodon lineatum (in part), Duméril, Bibron and Duméil, Érpétologie Générale, 7(pt. 2):936-938, February 25, 1854.

Conophis vittatus Peters, Monatsb. Akad. Wiss. Berlin, pp. 519-520, pl.,

fig. 3, October, 1860; Cope, Proc. Amer. Philos. Soc., 11:162, 1870; Bocourt *in* Duméril, Bocourt and Mocquard, Mission Scientifique au Mexique et dans l'Amerique Centrale, 2:644-646, pl. 38, fig. 7, 1886; Günther, Biologia Centrali-Americana, p. 165, March, 1895; Boulenger, Catalogue of the Snakes in the British Museum (Natural History), 3:123-124, 1896; Cope, Amer. Nat., 30:1024, 1896; Ann. Rept. U. S. Natl. Mus. for 1898, pp. 1094-1095, 1232, 1900; Gadow, Proc. Zool. Soc. London, 2:225, 1905; Amaral, Mem. Inst. Butantan, 4:211, 1929; Gadow, Jorullo, p. 55, 1930; Smith, Zool. Ser. Field Mus. Nat. Hist., 24:31-32, January 30, 1939; Taylor and Smith, Univ. Kansas Sci. Bull., 25:252-253, pl. 23, July 10, 1939; Stuart, Contr. Lab. Vert. Biol. Univ. Michigan, 65:23, March, 1954; Alvarez del Toro, Reptiles de Chiapas, pp. 153-154, 1960.

Conophis lineatus Cope, Proc. Acad. Nat. Sci. Philadelphia, 16(3):167, 1864 [*nec* Duméril, Bibron and Duméril, Érpétologie Générale, 7(pt. 2):936-938, atlas, pl. 73, February 25, 1854; specimen from Colima]; Sumichrast, Arch. Sci. Nat., p. 246, 1873.

Tomodon vittatus, Bocourt, Journ, de Zool., p. 407, 1876.

Conophis sumichrasti sumichrasti Cope, Journ. Acad. Nat. Sci. Philadelphia, ser. 2, 8:137, 1876 (Types.—United States National Museum, nos. 29123, 30258; type locality.—Tehuantepec, México); Bull. U. S. Natl. Mus., 32:77, 1887; Smith and Taylor, Univ. Kansas Sci. Bull., 33(pt. 2):334, March 20, 1950; Maldonado-Koerdell, Inst. Mexicanos Recursos Nat. Renov., p. 124, 1953.

Conophis sumichrasti viduus Cope, Journ. Acad. Nat. Sci., Philadelphia, ser. 2, 8:137, 1876 (Type.—United States National Museum, no. 30259; type locality.—Tehuantepec, México); Bull. U.S. Natl. Mus., 32:77, 1887; Cochran, Bull. U. S. Natl. Mus., 220:167, 1961.

Conophis sumichrasti, Cope, Proc. Amer. Philos. Soc., 18:271, August 11, 1879; Sumichrast, Bull. Soc. Zool. France, p. 182, 1880; Cope, Trans. Amer. Philos. Soc., 18:194, April 15, 1895; Cochran, Bull. U. S. Natl. Mus., 220:167, 1961.

Tachymenis lineata (in part), Garman, Mem. Mus. Comp. Zool., 8:60-61, July, 1884.

Conophis vittatus sumichrasti, Cope, Ann. Rept. U. S. Natl. Mus. for 1898, p. 1095, 1900.

Conophis vittatus videns Cope, Ann. Rept. U. S. Natl. Mus., for 1898, p. 1095, 1900 (apparent *lapus* for *viduus*).

Conophis vittatus vittatus, Cope, Ann. Rept. U. S. Natl. Mus. for 1898, p. 1095, 1900; Smith, Journ. Washington Acad. Sci., 31:119-120, March 15, 1941; Proc. U. S. Natl. Mus., 92:395, November 5, 1942; Proc. U. S. Natl. Mus., 93:408, October 29, 1943; Ann. Carnegie Mus., 30:91, November 2, 1944; Smith and Taylor, Bull. U. S. Natl. Mus., 187:44, October 5, 1945; Smith, Rev. Soc. Mexicanos Hist. Nat., 7:71, December, 1946; Smith and Taylor, Univ. Kansas Sci. Bull, 33(pt. 2):331, March 20, 1950; Davis and Smith, Herpetologica, 8:134, January 30, 1953; Maldonado-Koerdell, Inst. Mexicanos Recursos Nat. Renov., p. 130, 1953; Peters, Occas. Papers Mus. Zool. Univ. Michigan, 554:22, June 23, 1954; Duellman, Occas. Papers Mus. Zool. Univ. Michigan, 560:15, October 22, 1954; Webb and Fugler, Herpetologica, 13:35, March 30, 1957; Duellman, Occas. Papers Mus. Zool. Univ. Michigan, 589:15, March 21, 1958; Zweifel, Amer. Mus. Novitates, 1949:2, 5, June 17, 1959; Duellman, Univ. Kansas Publ. Mus. Nat. Hist., 15(1):91-92, December 20, 1961.

Conophis vittata, Gadow, Proc. Zool. Soc. London, 2:196, 1905; Through Southern Mexico, p. 181, 1908.

Conophis viduus, Smith, Zool. Ser. Field Mus. Nat. Hist., 24:31, January 30, 1939; Hartweg and Oliver, Misc. Publ. Mus. Zool. Univ. Michigan, 47:26-27, July 13, 1940.

Conophis vittatus viduus, Smith, Journ. Washington Acad. Sci., 31:120-121, March 15, 1941; Proc. U. S. Natl. Mus., 92:395, November 5, 1942; Proc. U. S. Natl. Mus., 93:408, October 29, 1943; Woodbury and Woodbury, Journ. Washington Acad. Sci., 34(11):370, 1944; Smith and Taylor, Proc. U. S. Natl. Mus., 187:44, October 5, 1945; Univ. Kansas Sci. Bull., 33(pt. 2):340, March 20, 1950; Werler and Smith, Texas Journ. Sci., 4:565, fig. 16, December 30, 1952; Maldonado-Koerdell, Inst. Mexicanos Recursos Nat. Renov., p. 130, 1953; Davis and Dixon, Proc. Biol. Soc. Washington, 72:82-83, July 24, 1959.

Conophis vittatus vittatus × *Conophis vittatus viduus,* Alvarez del Toro and Smith, Herpetologica, 12:13, March 6, 1956.

Type.—Zoologisches Museum Berlin. Type locality not given, for the specimen was purchased from a dealer in Hamburg. The type locality was first restricted to "Acapulco," Guerrero, by Smith (1941:119), then to Laguna Coyuca, Guerrero, México, by Smith and Taylor (1950:331).

Diagnosis.—Three or four dorsal dark stripes, each involving two or more adjacent scale-rows; never having brown or black on the 1st scale-row; seven supralabials immaculate white or pale tannish-white.

Variation.—One hundred seventy-one specimens have 149 to 181 (163.7±6.33) ventrals. One hundred fifty-three of these having complete tails have 55 to 76 (64.8±4.90) subcaudals; the number of ventrals plus subcaudals varies from 214 to 245 (228.5). In 170 specimens the reduction from 19 to 17 dorsal scales takes place between ventrals 84 and 118 (102.3±6.60). Sexual dimorphism is evident in the number of subcaudals; 58 females have 55 to 66 (60.0) and 95 males have 59 to 76 (67.8) subcaudals. The longest specimen (AMNH 68004) is a male from Escurano, Oaxaca, México, having a body length of 668 mm., a tail length of 182 mm. and a total length of 840 mm. A juvenile (CNHM 40435) from Tehauntepec, Oaxaca, México, has a body length of 133 mm., a tail length of 31 mm. and a total length of 164 mm.

Variation in coloration is of such magnitude that it has been used as the basis for recognition of subspecies. Unfortunately, until this time, most specimens reported upon in the literature represented the two extremes of variation. After examining the coloration of 174 specimens with respect to geographic distribution, I conclude that only one highly variable species is represented. Specimens from the northern and western parts of the range (Michoacán, Colima, and Durango) have the color pattern of *C. vittatus* as described by Peters (1860:518-521); these snakes have four narrow black stripes on a white or pale tan background, and an immaculate white venter. The lateral dark stripe, which on the head passes through the eye, is present on the dorsal half of the 3rd and the ventral half of the 4th scale-rows; the dorsolateral dark stripe, which passes along the middle of the head and splits on the nape, is present on the middle of the 8th scale-row. The other extreme in color pattern consists of three broad stripes; the two dorsolateral stripes are fused. This pattern is prevalent in specimens from the area around Tehuantepec, Oaxaca. The lateral stripes include the dorsal half to two-thirds of the 2nd, all of the 3rd and 4th, and half of the 5th scale-rows; the fused dorsolateral stripes sometimes cover all of the area dorsal to and including the dorsal third of the 7th scale-row.

Snakes from areas between Tehuantepec and the margins of the distribution

of this species are variously intermediate between the extremes described above. In some snakes from these areas the lateral stripes are broad and include either the dorsal half of the 2nd scale-row or the ventral half of the 5th scale-row, but not both on the same specimen. Also, the dorsolateral stripes are broad and include most of the 9th and a part of the 10th scale-rows. Many specimens from the area around Tehuantepec, where the three-striped pattern is prevalent, have an intermediate pattern. Some have white on the center of the 10th scale-row or lateral stripes that are not so broad as to include the 3rd and 4th and half of each of the 2nd and 5th scale-rows.

The supralabials are immaculate white or pale tan, except that in some specimens the dorsalmost part of some supralabials are dark brown or black as they are included in the ventral boundary of the dark stripe that passes through the eye. There are no dusky markings on the chin or on any of the ventral scales.

There is no ontogenetic change in color pattern; juveniles have the same coloration as adults from the same geographic area.

Color in life is not greatly different from that of preserved specimens. One specimen (UMMZ 114483) from 10.8 miles south of Oaxaca, Oaxaca, had in life black stripes, a pale yellowish tan dorsal ground-color and a pale off-white venter.

An excellent photograph of this species appears in Schmidt and Inger (1957:230) under the name *Conophis lineatus*.

Remarks.—I have been unable to find variation of geographic importance in scutellation in this species. A wide range of variation in the characters of scutellation is present in specimens from most localities; it shows no significant clinal or geographic trends. As I have stated previously, in the discussion of variation, coloration has been the feature primarily used by previous workers to distinguish two "subspecies" for this species; *C. vittatus vittatus* having four black stripes and *C. vittatus viduus* having three black stripes. Most of the three-striped snakes occur in the vicinity of Tehuantepec, Oaxaca, whereas the four-striped snakes are found near the margins of the range of the species in Durango, Colima, Michoacán, Morelos and Puebla. Specimens that would have to be considered intergrades between the "subspecies" are found in Michoacán, Guerrero, Oaxaca and Chiapas. At the time the subspecies were proposed only specimens from Tehuantepec or from marginal areas were known. Utilizing the large number of specimens of this species presently available, geographic variation is found to be clinal, from those with three stripes from near Tehuantepec, through several intermediate patterns present on specimens from single localities in Guerrero, Oaxaca and Chiapas, to those with four dark stripes in areas farthest removed to the north and west from Tehuantepec. Since only coloration shows geographic variation, and since this variation represents a continuous cline, subspecies cannot be recognized for this species.

The presence and position of the three or four dark stripes on the body and the absence of brown on the 1st scale-row or on the ventral scales, in combination with the generic characters, distinguish *Conophis vittatus* from all other Méxican snakes. The only other snake that occurs in western México that has been confused with *C. vittatus* is *Coniophanes piceivittus taylori*, which has 25, instead of 19, scale-rows.

Distribution.—Semi-arid habitats on Pacific slopes from extreme southern Durango southeastward to Tuxtla Gutierrez, Chiapas, and inland in the eastern Balsas Basin to Morelos and western Puebla (fig. 5).

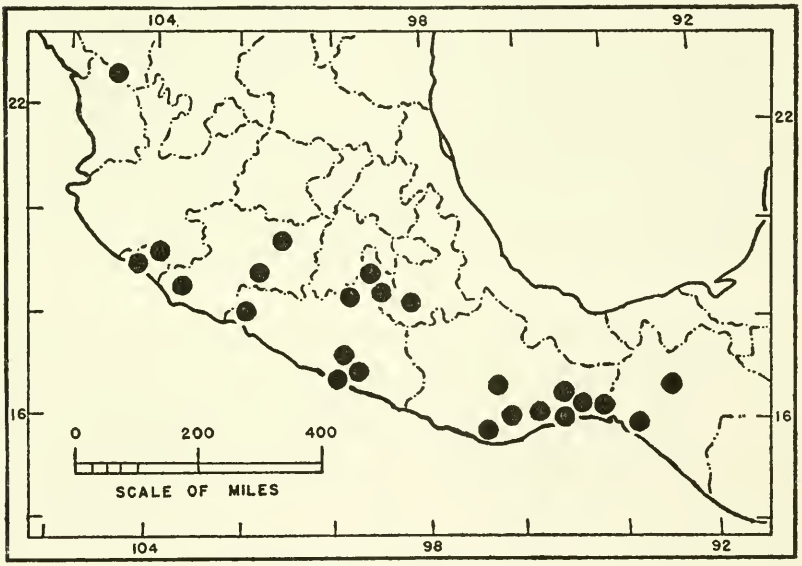


FIG. 5. Selected locality records for *Conophis vittatus*.

Specimens examined.—Total of 174, as follows: MÉXICO: *no specific locality*, AMNH 66150-52, SU 9465. *Chiapas:* Piedra Parada, USNM 121453. *Pizo de Oro*, UIMNH 40821. Tuxtla Gutierrez, Parque Madero, UIMNH 37992-93, 38036-37. *Colima: no specific locality*, MCZ 46860, USNM 31394, 31396-97. 1 mi. SW Colima, AMNH 12783. S of Manzanillo, AMNH 19641. *Durango:* Hacienda de Gabriel, AMNH 14217. *Guerrero: Acahuizotla*, TCWC 7419, 9469. *1 mi. W Acahuizotla*, TCWC 7418. 3 mi. W Acapulco, AMNH 71626. *6 mi. E Acapulco*, TCWC 9476-77. *10 mi. S Acapulco*, TCWC 8578. *Agua del Obispo*, CNHM 104948, TCWC 11586. Near Chilpancingo, MVZ 45067, UMMZ 85722-23. *1 mi. SW Colotlipa*, TCWC 9471-74. *2 mi. SW Colotlipa*, TCWC 9475. 14 mi. S Ixtapán de la Sal, KU 67648. *Laguna Coyuca*, CNHM 25881, UMMZ 80942. near La Unión, AMNH 66337. *Magueyes, Laguna Coyuca*, AMNH 66149. *Playa Encantada*, TCWC 9470. 1 mi. S Tierra Colorada, KU 67649. near *Xaltinanguis, km. 405*, CNHM 104947. *Michoacán:* Coalcomán, UMMZ 104693. *½ mi. SE Coalcomán*, UMMZ 104492. *1 mi. N. Coalcomán*, UMMZ 112543. *1 mi. NE Coalcomán*, UMMZ 104692. Puerta de la Playa, UMMZ 105155. 12 mi. S

Tzitzio (by road), UMMZ 99153. *Morelos: 12 km. NW Axochiapan,* TCWC 7311, UIMNH 17613, 25924. 7 mi. SE Cuernavaca, MVZ 32258. *Huajintlán, km. 133,* CNHM 103270. 12 km. S Puente de Ixtla, km. 133, CNHM 104949. *Oaxaca: Bisiliana,* AMNH 68010. *near Caoba, foot of Cerro Arenal,* AMNH 68009. *Cerro Arenal,* AMNH 68000-03. *Cerro de Laollaga,* UIMNH 36213. *Cerro de San Pedro,* UIMNH 17616. *Cerro Palma de Oro,* UIMNH 37116. *"C. Madrena, Sto. T. Quieri,"* UIMNH 46904. near Chivela, MCZ 25021. Cinco Cerros, UIMNH 37114. *Dami Liesa,* AMNH 66877, UIMNH 6158, 37115. *Escuranos,* AMNH 66873-74, 68004-06. *Finca Santa Teresa, 2 km. NW Tehuantepec,* UMMZ 82648. *Huilotepec,* AMNH 66878, UIMNH 40820. *between Huilotepec and Tehuantepec,* AMNH 65106, UMMZ 82644-45. *Las Tejas,* UIMNH 6151-54. *Mixtequilla,* UIMNH 6157, 36211. *between Mixtequilla Mountains and Tehuantepec,* UMMZ 82652. *between Niltepec and "Carixxal,"* AMNH 66876. 10.8 mi. SE Oaxaca, UMMZ 114483. *Quiengola,* UIMNH 17617. *between Quiengola Mountains and Tehuantepec,* UMMZ 82647. *Rancho Poso Río, 6 km. S Tehuantepec,* UIMNH 6144-49, 37117-19, UMMZ 82649-51. *Rincón Bamba,* CNHM 105129-30, UIMNH 17615. *Salazar,* AMNH 66875. *vicinity of Salina Cruz,* UMMZ 82653. *San Gerónimo,* AMNH 4306, CNHM 1457. *San Lucas Ixtepec,* UIMNH 36206. San Juan Lajarcia, UIMNH 36212. San Mateo del Mar, AMNH 65914. *San Pablo,* UIMNH 36207. *Santa María (Cerro de Liesa),* AMNH 68011. Tapanatepec, MCZ 27806-11. Tehuantepec, AMNH 19644, 65107-09, 65907-13 plus 7, 66871-72, 66879, 68007-08, CNHM 40435-36, 105126-28, MCZ 46403, UIMNH 6150, 17614, 17618, 29692, 36208, 37120-21, UMMZ 82642-43, 82646, USNM 109709-14, *1-2 leagues SSE Tehuantepec,* UMMZ 82639-41. Tenango, UIMNH 36209-10. between Tlacolulita and Tequisistlán, CNHM 105125. *Yerba Santa,* UIMNH 6155-56. *Puebla:* Atencingo, KU 39626.

Skull

In studying the osteology of the genus *Conophis,* I have examined two complete skeletons (one *C. vittatus* and one *C. lineatus*); two additional skulls of *C. vittatus* and *C. lineatus*; and 24 sets of dentigerous bones, representing all of the species. Terminology of the skeletal elements is that of Duellman (1958), Parker (1878), Radovanovic (1937) and Szunyoghy (1932). The drawing of the right side of the skull of a specimen of *Tomodon lineatus* that appears in Jan and Sordelli (1881:liv. 50, pl. 2, fig. 34) is of little value due to its small size and lack of detail.

The skull of *Conophis* is typical of a relatively unspecialized colubrid snake. Skulls of *Conophis lineatus concolor* and *C. vittatus* closely resemble each other. The following description is based primarily on the skull of *C. lineatus concolor* (UMMZ S-778).

The elements are discussed in the following order: nasal region, cranium and associated elements, maxillo-palatal-pterygoid arch, mandible, dentition, and vertebrae.

Nasal region.—The premaxillary is relatively heavy and has a concavity posteroventrally. The lateral processes slope downward, but remain fairly thick, and do not project far laterally. This shape (fig. 6) tends to strengthen the nasal region; this anterior strengthening may be a reflection of the fossorial habits of these snakes. There are no posterior processes of the premaxillary; thus the line of fusion with the nasals and septo-maxillaries is broad. The

nasal plate is more than twice as long as wide. The nasals are relatively flat above, although each curves slightly downward medially and fuses into the medial nasal septum; laterally each nasal is narrower and deflected downward, forming a small dorsal shield over the nasal cavity. The septo-maxillaries are closely associated with the vomers and form the cavity in which the organ of Jacobson is situated. The broad medial part of the septo-maxillary forms the roof and anterior border of the cavity, whereas the anterior part of the vomer contains the main part of the capsule and forms the posterior and most of the lateral borders of the cavity. The vomer has a thin anterior ridge that gradually disappears before it reaches the border of the premaxillary. The

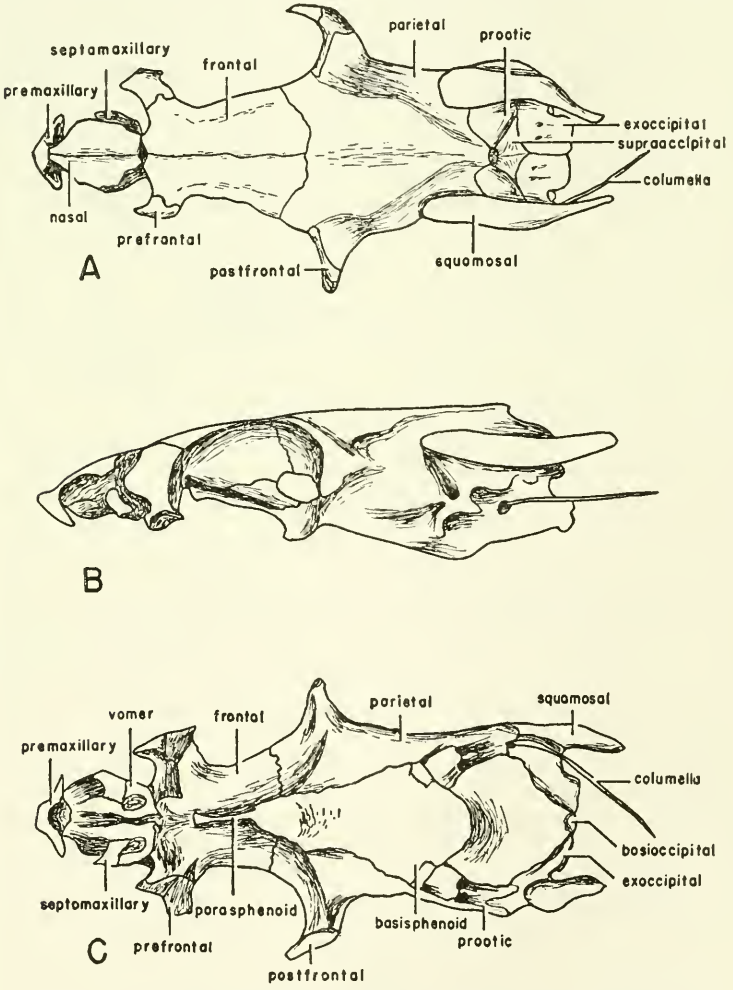


FIG. 6. The skull, lacking dentigerous bones, of *Conophis lineatus concolor* (UMMZ S-788) showing (A) dorsal, (B) lateral, and (C) ventral views. ×3.

vomer is approximately U-shaped, when viewed from below. It has no posterior process and does not articulate with the parasphenoid; there is a sizeable gap between the two bones. The septo-maxillary has a lateral process that terminally is directed slightly anteriorly.

Cranium and associated elements.—The frontal is almost three times as long as it is wide; it is flat above with an emarginate dorsolateral margin that forms the upper limit of the optic capsule. Ventrally the frontal is concave and forms the median limits of the optic cavity. Farther ventrally the frontal joins with the parasphenoid, which at this place forms the ventral extent of the skull, and together with the basisphenoid forms the ventral part of the posterior three-fourths of the skull. In ventral aspect, the parasphenoid is a long, thin bone, slightly expanded anteriorly. It forms the anterior floor of the optic foramen; whereas the frontal forms the anterior roof of the same opening. The frontal and its septo-maxillary process surround the olfactory fenestra. The prefrontal articulates with the anterolateral process of the frontal. The posterior surface of the prefrontal forms the anterior wall of the orbit of the eye. The articulating surface upon which the median process of the maxillary bone rests is situated ventrally. The anterior dorsal surface of the prefrontal, together with the anterolateral edge of the frontal, extends slightly over the nasal cavity, affording some degree of protection for the contained organs and forming the posterior border of the cavity. A small nasal process also extends anteriorly from the ventrolateral surface of the prefrontal. The orbital-nasalis foramen is located in the anterior surface of the prefrontal. The parietals are fused into one large bone that forms the roof and sides of the middle part of the cranial cavity. From its suture with the frontal, the dorsal surface of the parietal is relatively flat in the area bounded laterally by the parietal crests, which extend posteromedially from the anterolateral corners of the bone and converge medially at a point near its posterior margin. A slight posterior extension of the parietal crests forms the supratemporal crest, which is present on the posterior part of the parietal and on the anterior part of the supraoccipital. The postfrontals are attached to the anterolateral processes of the parietal. Together the anterior surfaces of these two bones form the posterior rim of the orbit of the eye. The postfrontal extends laterally and ventrally and has a terminal extension that projects anterolaterally. In an articulated skull the transpalatine articulates with the ventrolateral articulating surface of the postfrontal. Anteromedially, the parietal forms the roof and posterior margin of the optic foramen. The basisphenoid, which is fused with the parasphenoid, also forms a small part of the posteroventral margin of the optic foramen. The basisphenoid forms the floor of the middle part of the cranial cavity and the ventromedial downpouching that contains the pituitary body. Posterolateral to the parietal and dorsal to the posterior part of the basisphenoid is the prootic. Laterally this bone is deeply emarginate; posteriorly it forms a large part of the otic notch, through which the columella passes. The columella is a long, thin bony rod that terminates posteriorly in cartilage. It is the cartilagenous part of the columella that connects with the external sound detecting mechanism. There are several foramina on the lateral surface of the prootic. On the anterolateral surface of the prootic, branches of the trigeminal nerve pass through three foramina whereas the facial nerve passes through the single posterior foramen

near the otic notch. The squamosal is attached dorsoventrally to the posterior part of the parietal and to the lateral part of the prootic. At this place of attachment there is on the prootic a relatively heavy crest that forms a rather broad articulating base. The squamosal is long, flat, and curves slightly in a dorsal direction throughout its length; it becomes thinner and narrower posteriorly. The posterior third of the squamosal forms a broad base by means of which the squamosal articulates with the quadrate. The columella and the squamosal extend posteriorly beyond the limits of the braincase. Posteriorly the skull consists of four bones: an unpaired median dorsal supraoccipital, an unpaired median ventral basioccipital and two lateral exoccipitals. The basioccipital does not have noticeable pterygoid processes, but is rather smooth ventrally and only slightly emarginate on its posterolateral margins. Posteriorly, this bone forms the ventral part of the occipital condyle. The rest of the condyle, on each side, is formed by the exoccipitals. The exoccipitals also form part of the base to which the squamosal is attached. The exoccipitals extend around the sides of the foramen magnum and meet dorsally. Each exoccipital also forms the posterior part of the otic notch, which traverses the exoccipital. The exoccipitals bear moderate occipital crests that extend

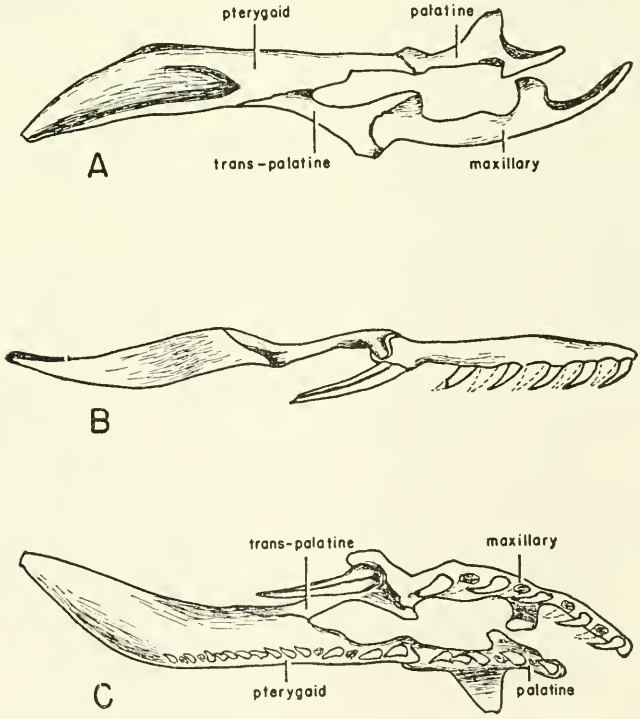


FIG. 7. The maxillo-palatal-pterygoid arch of *Conophis lineatus concolor* (UMMZ S-788) showing (A) dorsal, (B) lateral, and (C) ventral views. × 3. Teeth shown by means of broken lines were represented only by their sockets.

posterolaterally across the supraoccipital as branches from the supratemporal crest. The supraoccipital also has a medial crest that extends a short distance posteriorly from the supratemporal crest onto the exoccipitals at their dorsal line of fusion.

Maxillo-palatal-pterygoid arch.—In an articulated skull, the anterior edge of the maxillary is immediately posterior to the lateral tip of the premaxillary (fig. 7). The maxillary is curved moderately laterally and is not robust at its tip, but it becomes heavier about one-third of its length posteriorly. A dorsomedian process begins at about one-third of its distance from the anterior end; the prefrontal articulates with this process. The process is broad and almost flat, except that at its medial end, an elongate, rounded knob extends ventrally. The dorsomedian process of the maxillary extends toward, but does not meet, a lateral process from the palatine. The maxillary teeth are set in sockets on the ventral surface of the bone. Just posterior to the level of the last prediastemal tooth is the median trans-palatine process that articulates with the anteromedian part of the trans-palatine. Immediately posterior to this process, the maxillary narrows slightly; then it broadens to form an obliquely oriented knob. The posteroventral surface of the posterior knob of the maxillary bears one or two enlarged maxillary teeth. (These teeth are discussed further in the section on Dentition.) The anterolateral part of the trans-palatine articulates with the dorsal surface of the posterior knob of the maxillary. Toward the middle of its length, the trans-palatine narrows considerably; then it broadens again and articulates with the pterygoid. The palatine is slightly rounded at its anterior end, which extends anteriorly to the posterior margin of the vacuity containing Jacobson's organ. The palatine extends posteriorly to the trans-palatine process of the maxilla, where the palatine articulates with the pterygoid. A posterior pterygoid process from the palatine projects posteromedially from the end of the palatine and overlaps the anterior end of the pterygoid. Just less than one-half the distance from the anterior end of the palatine, there is a lateral process that curves ventrolaterally forming a blunt tip posteriorly. Slightly more posteriorly and on the medial side of the palatine, is a medial sphenoid process, which is thin, rather broad, and curves ventromedially; ultimately it comes to lie near the anterior part of the parasphenoid. The palatine teeth are set in shallow sockets on the ventral edge of the bone. Of the bones of the maxillo-palatal-pterygoid arch, those on the pterygoid extend farthest posteriorly. The pterygoid is broad medially and posteriorly, although pointed at its posterior tip. The trans-palatine articulates in a broad line at about one-third of the distance along the lateral margin of the pterygoid. Immediately posterior to this articulation, there is a median ridge on the pterygoid; lateral to the pterygoid ridge is an abrupt hollow, the pterygoid groove. Posteromedially, this groove becomes gradually more shallow and disappears. The dorsal surface of the pterygoid is rounded anteriorly and somewhat flattened posteriorly, whereas the ventral surface is gently rounded along its length, except that there is a high median crest. The pterygoid teeth are situated in shallow sockets along this crest. The teeth diminish in size posteriorly.

Mandible.—The dentary (fig. 8) is compressed laterally and rounded below. The teeth, which are longest about one-third of the way from the anterior end of the dentary, are set in sockets on the medial side of the bone.

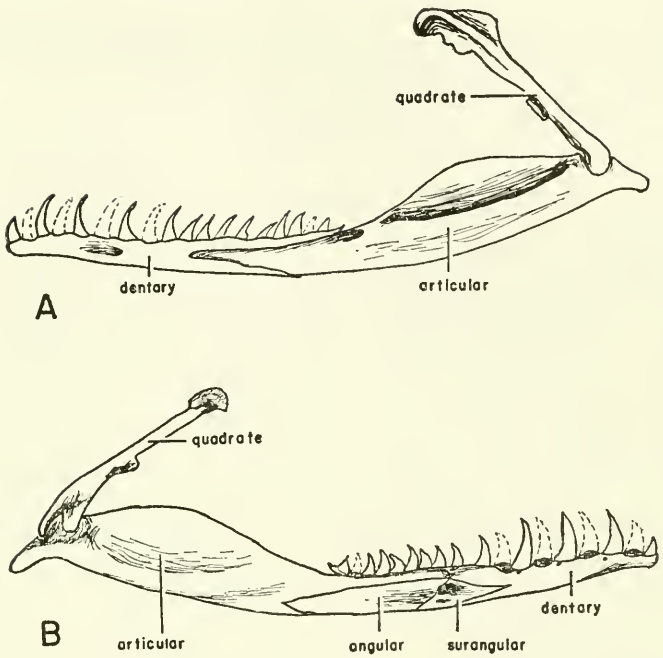


FIG. 8. The left mandible and associated quadrate of *Conophis lineatus concolor* (UMMZ S-788) showing (A) lateral and (B) medial views. × 3. Teeth shown by means of broken lines were represented only by their sockets.

The posterior half of the dentary overlies the fused surangular-prearticular part of the articular. Ventrally, the posterior part of the dentary underlies the splenial, which is set in a median trench within the dentary. Near the common suture of the dentary and the splenial is the large inferior alveolar foramen; completely within the splenial and ventral to the inferior alveolar foramen is the anterior mylohyoid foramen. Posterior to the splenial and also forming a part of the ventral surface of the mandible is the wedge-shaped angular, which lies directly beneath the fused surangular-prearticular. As has been implied, the articular, the surangular, and the prearticular are fused. The prearticular part of this bone forms a part of Meckel's canal. In the surangular part, immediately posterior to the end of the dentary, is the large surangular foramen. Lying in a longitudinal axis along the medial surface of the articular is a high crest, dorsal to which is a deep hollow. The lateral wall of the articular above this hollow is thin and rounded dorsally; the ventral surface is uniformly round and slightly curved dorsally, except that it ends with a short tympanic crest, which projects beyond the articulation with the quadrate. Where the quadrate articulates with the dorsolateral surface of the posterior portion of the squamosal, the former is broad and has a high midlateral crest, which extends about one-third of the distance down the quadrate before disappearing. The columellar process (the place of fusion of the

columella) is about two-thirds of the way down the medial surface of the quadrate. Ventrally the quadrate has a narrow neck dorsal to its articulation with the articular. The articulation is formed by two lateral flanges of the quadrate that fit over a medial ridge formed by the articular.

Dentition

Teeth on the maxillary and pterygoid decrease in size posteriorly, whereas those of the dentary do likewise except for the first one or two that are usually slightly smaller than those immediately posterior. The palatine teeth are subequal in size. The enlarged, grooved teeth on the maxillary are in shallow sockets on the posteroventral surface of the posterior knob of the maxillary. These teeth point posteriorly. The grooves are deep and are situated anterolaterally. One or two enlarged grooved teeth are present on a given maxillary. There seems to be a correlation between the type of preservation, the age of the snake, and the number of grooved teeth. Old (large) individuals always have only one grooved tooth that is rooted and functional, whereas some of the younger animals have two in place. Usually replacement teeth are present in alcoholic specimens, but these unrooted teeth are lost in the preparation of dried skeletons. Thus, it seems that in *Conophis* only one pair of grooved teeth is functional at any one time, although usually replacement teeth are present behind and beside the functional one. Some specimens have one tooth in the medial socket on one side and one in the lateral socket on the other. Replacement teeth on the maxillary and dentary are present in the buccal tissue on the medial side of the bones, whereas on the palatines and pterygoids, the replacement teeth are present laterally. Apparently there are no significant differences in dentition among the members of the genus *Conophis*.

Vertebrae

The fiftieth vertebra of *Conophis vittatus* (UMMZ 82642) can be described as follows: The neural spine is elongate, thin and low; the posterior edge is sharply emarginate, and the anterior edge is only slightly emarginate. The zygosphene is thin dorsoventrally; in a ventral or dorsal view the zygosphene has a slightly concave anterior edge, the flat surface of which is oriented ventrolaterally. The centrum is elongate and triangular from below; it is widest at the paradiapophyses and narrowest at the short condylar neck. The condylus is directed posteriorly. The centrum, when viewed laterally, is slightly concave and has prominent subcentral ridges that extend from the median side of the paradiapophysial articular surfaces posteriorly to the neck of the condylus. The paradiapophysial articular surfaces are well developed and have two facets. The diapophysial surface is larger and more spherical than the parapophysial one. The parapophysial process projects beyond the parapophysial articular surface and is nearly even with the lip of the cotyle, which is slightly oval. The neural arch is slightly depressed; its width is somewhat less than the width of the cotyle. The articular surfaces of the postzygapophyses are oval and are directed posterolaterally. There is a strongly developed concave interzygapophysial ridge. A well-developed accessory spine extends laterally beyond the oval articular facets of the prezygapophysis and forms a slightly flattened, blunt spine. Excellent drawings

of the middle thoracic vertebra of *Conophis lineatus dunni* from Honduras were published by Auffenberg (1958:6).

Hemipenes

The hemipenes of *Conophis* are moderately caliculate, having spines covering the surface from the base to near the apex (fig. 9). These spines are largest near the base and are reduced to small papillate projections near the apex. The apex terminates in a small disc having three to five laminae in *C. vittatus* and one lamina in *C. lineatus concolor.* The sulcus is bifurcate; the fork is near the base and almost gives the appearance of two sulci on some specimens. Distally the apices are widely separated, and the intervening space gives the hemipenis a slightly bilobed appearance in some species (especially *C. vittatus*) or a deeply bilobed appearance in others (especially *C. lineatus concolor*).

FIG. 9. The everted left hemipenis of *Conophis vittatus* (UMMZ 82650). × 5.

The everted hemipenis reaches posteriorly to the eighth subcaudal scale. The sulcus bifurcates at the third subcaudal scale. The situation is similar *in situ* (Cope, 1895:pl. 28, fig. 2).

There are no apparent hemipenial differences among the species of the genus *Conophis.* As can be seen in the above description, the hemipenis of *C. vittatus* is less bilobed and has a more pronounced disc at the apex than the others. The hemipenis of *C. lineatus concolor* is most bilobed, but has the smallest apical disc. The other species and subspecies vary widely within these extremes.

Food and Feeding

Conophis eats mostly small lizards, especially *Cnemidophorus.* In México *Conophis* occurs in semi-arid habitat where *Cnemidophorus* is common. A specimen each of *Conophis vittatus* and *C. lineatus lineatus* were obtained while I was collecting *Cnemidophorus.* The only record of *Conophis* having fed on a warm-blooded vertebrate was obtained in the course of this study, when I recovered from the stomach of a *Conophis lineatus concolor* (CNHM 36299) from Chichén Itzá, Yucatán, a heteromyid rodent (*Heteromys gaumeri*).

Ralph Axtell (personal communication) observed *Conophis* actively searching for food at dusk. His observations were made near Tehuantepec, Oaxaca, and the snakes were seen to chase lizards of the genus *Cnemidophorus*. Near Alvarado, Veracruz, in the late afternoon, I watched a *Conophis lineatus lineatus* follow a lizard into a hole.

Mittleman (1944:122) presents the only discussion of the mode of feeding of a captive specimen of *Conophis lineatus* ssp. When presented with a *Thamnophis* slightly smaller than itself, the *Conophis* struck, and within eight minutes immobilized the *Thamnophis*. Within one-half hour the *Thamnophis* was swallowed. Three days later the *Conophis* ate another *Thamnophis*, though still distended from its first meal; nine days later it ate a *Storeria*. In the course of several months, the *Conophis* ate various toads and hylids and two more *Storeria*. Apparently members of the genus *Conophis* do not constrict their prey, but rely upon a combination of loss of blood and action of the venom to completely immobilize their prey.

Ditmars (1931:pls. 26-27) showed three photographs of "*Conophis lineatus*" (actually *Conophis pulcher*) ingesting another snake, identified by him as a young *Ophis* (= *Xenodon*) *colubrinus*.

Effect of Poison

The rear fangs of these snakes are large for the size of the snake. Various collectors have been bitten, and several reports of the effect of the poison have been published. The snakes are aggressive and bite constantly while being handled. A field companion, Dale L. Hoyt, was bitten on the forefinger by a specimen of *C. l. lineatus* and immediately felt a burning sensation. The finger swelled, much as it would if stung by a wasp, but it returned to normal size in about twenty-four hours. Ditmars (1931:legend pl. 27) reported immediate burning pain and a localized swelling, an inch in diameter and half an inch high, which lasted for several hours. Mertens (1952b:83) reported merely that the hand of the gardener at the Instituto Tropical in San Salvador bled strongly for a full hour. Edward H. Taylor was bitten by a specimen of *Conophis vittatus* (Taylor and Smith, 1939:252); pain and swelling lasted for some time. Taylor (personal communication) is still troubled by damage incurred by that bite, which apparently resulted in mechanical damage to the second joint of the middle finger, for the joint swells when the finger is used or exercised. William E. Duellman (personal communication) was bitten on the hand in July,

1956. There was immediate pain and localized swelling, both of which disappeared several hours later.

TAXONOMIC RELATIONSHIPS AND EVOLUTION

The genus *Conophis* is known only from the Recent. Except that *Conophis* belongs to the subfamily xenodontinae and probably is of New World origin, little is known about the relationships of the genus. Auffenberg (1958) described a new genus and species of fossil colubrid snake from the Miocene of Montana as *Dryinoides oxyrhachis* and compared it with several recent genera. This specimen, of which there is a relatively complete skull and a series of vertebrae, seems most closely to resemble a specimen of *Conophis lineatus dunni* (UF 7657) from Honduras, with which it was compared in basic osteology. The two genera could be related, for the progenitors of *Conophis* possibly inhabited much of North America in the Miocene.

Another possibility is that the main stock of the xenodontines reached South America in earliest Tertiary times, and that the formation of the Panamanian and Colombian seaways that separated South America and Central America from the Late Paleocene to the middle of the Pliocene left the *Conophis* stock isolated in Middle America where members of the genus dispersed through semi-arid habitats.

Turning our attention now to the species within the genus, instead of the genus as a whole, *Conophis vittatus* is readily set apart from other members of the genus on the basis of the universal presence of seven supralabials. In basic coloration it also differs, having no stripe on the 1st scale-row, or spots on the venter, and a maximum of four broad stripes on the body. The other species appear to be more closely related; these make up the *C. lineatus*-group. *Conophis nevermanni* differs so much from the other species that it might be placed in a separate group. Nevertheless, the basic striped pattern, which is masked by the increased melanism of many specimens, indicates that *nevermanni* is more closely related to the *lineatus*-group than to *vittatus*. The *lineatus*-group, thus, consists of *pulcher*, *nevermanni* and the three subspecies of *lineatus*. In this group the color pattern is characterized by the high frequency of ventral spotting, darkening of part of the supralabials, dark pigmentation on the 1st scale-row, and more than four dark stripes on the body of adults. *Conophis lineatus concolor*, on which the dark pigmentation on the body apparently is secondarily lost, is an exception.

If differences in color pattern be used as an indication of the relationships between the species and subspecies of the genus *Conophis,* I would consider *C. vittatus* the most divergent unit. The subspecies of *lineatus* closely resemble one another and, as a unit, resemble *pulcher* from which they differ primarly in the position of the dorsalmost stripes. *Conophis nevermanni* is more divergent than is *pulcher* from the species *lineatus,* but probably is not so far removed from *lineatus* as is *vittatus.*

In the light of what has been pointed out immediately above with respect to resemblances of, and differences between, the species, an hypothesis to account for their formation and for their presence in the areas where they are today is the following: Concurrent with climatic fluctuations in the Late Pliocene and Pleistocene, the northernmost population differentiated into the species *vittatus,* and has subsequently spread north and west from the region of Tehuantepec, México. During the same period *nevermanni* became isolated in northern Costa Rica.

The species *pulcher* probably differentiated from the remaining *lineatus* stock during the Early Pleistocene orogenic upheaval in Guatemala. The *pulcher* stock was isolated on the Pacific Coastal slopes of Guatemala, while *lineatus* moved through the subhumid corridor of northern Middle America into México and southward toward Costa Rica (Stuart, 1954a). In the Late Pleistocene and Recent, *pulcher* moved back across the central Guatemalan highlands occupying its present range in northern Middle America. Primarily because of the formation of unsuitable habitat (wet forest) that presently separates the geographic ranges of populations of *lineatus,* this species differentiated into three subspecies.

SUMMARY

The genus *Conophis* Peters, 1860, contains four species. Three are monotypic and the fourth has three subspecies, making a total of six taxa.

The genus is characterized by maxillary teeth of equal size followed by a diastema and two enlarged grooved fangs. The scales are smooth, in 19 rows at mid-body, and 17 nearer the tail. The anal is divided, apical pits are lacking, the head shields are normal for a colubrid, and the hemipenis is bilobed having many large basal spines.

The six taxa are separated primarily on the basis of color pattern, but characters of scutellation, including numbers of dorsals, ven-

trals, caudals, and places of reduction of the number of dorsal scale-rows, were analyzed.

Snakes of this genus are distributed throughout semi-arid environments from southern México southward into Costa Rica. They feed upon lizards, primarily of the genus *Cnemidophorus;* in addition they are known to eat small rodents and other snakes.

Conophis is a member of the subfamily Xenodontinae and, as presently understood, has no known living close relatives. A single specimen of *Dryinoides* from the Miocene of Montana has been compared with this genus. The genus *Conophis* is thought to have evolved in Middle America. The present distribution and differentiation probably are primarily the result of climatic fluctuations in Middle America, which produced the areas of subhumid environment where *Conophis* presently lives.

LITERATURE CITED

AUFFENBERG, W.
1958. A new genus of colubrid snake from the Upper Miocene of North America. Amer. Mus. Novitates, 1874:1-16. February 27.

COPE, E. D.
1861. Contributions to the ophiology of Lower California, México and Central America. Proc. Acad. Nat. Sci. Philadelphia, 13:292-306. December 28.

1867. Fifth contribution to the herpetology of tropical America. Proc. Acad. Nat. Sci. Philadelphia, 18:317-323. February 20.

1871. Ninth contribution to the herpetology of tropical America. Proc. Acad. Nat. Sci. Philadelphia, 23(2):200-224. October 24.

1876. On the batrachia and reptilia of Costa Rica. Journ. Acad. Nat. Sci. Philadelphia, series 2, 8(4):93-154, 6 pls.

1895. The classification of the ophidia. Trans. Amer. Philos. Soc., 18:186-219, 33 pls. April 15.

1900. The crocodilians, lizards, and snakes of North America. Ann. Rept. U. S. Natl. Mus. for 1898, pp. 153-1270, 36 pls.

DITMARS, R. L.
1931. Snakes of the World. New York, The MacMillan Company, 1931. xi + 207 pp., 84 pls.

DOWLING, H. G.
1951. A proposed standard system of counting ventrals in snakes. British Journ. Herpetology, 1(5):97-99, fig. 1.

DUELLMAN, W. E.
1958. A preliminary analysis of the herpetofauna of Colima, Mexico. Occas. Papers Mus. Zool. Univ. Michigan, 589:1-22, March 21.

DUMÉRIL, A. M. C., BIBRON, G., AND DUMÉRIL, A. H. A.
1854. Érpétologie générale, ou histoire naturelle des reptiles. Paris, 7(pt. 2):xii + 785. February 25. Atlas, 24 pp., 108 pls.

DUMÉRIL, A. H. A., BOCOURT, M., AND MOCQUARD, F.
1870-1909. Mission Scientifique au Mexique et dans l'Amerique Centrale . . . Etudes sur les Reptiles. Paris, vol. 2:xiv + 1012 pp., 77 pls.

GARMAN, S.
1884a. The North American reptiles and batrachians. Bull. Essex Inst., 16:1-46. January 9.

1884b. The reptiles and batrachians of North America. Mem. Mus. Comp. Zool., 8(3):xxxi + 185 pp., 9 pls. July.

GÜNTHER, A. C. L. G.
1858. Catalogue of colubrine snakes in the collection of the British Museum. London. xiv + 281 pp.

HUXLEY, J.
1942. Evolution. The Modern Synthesis. London. 645 pp.

JAN, G. AND SORDELLI, F.
1866. Iconographie Generale des Ophidiens. Milano. livr. 19, pls. 1-6. December.
1881. Iconographie Generale des Ophidiens. Milano. livr. 50, pls. 1-7. November.

MAYR, E.
1942. Systematics and the Origin of Species. New York, x + 334 pp., 29 figs.

MAYR, E., LINSLEY, E. G., AND USINGER, R. L.
1953. Methods and Principles of Systematic Zoology. New York. ix + 328 pp., 45 figs.

MERTENS, R.
1952a. Neues uber die Reptilienfauna von El Salvador. Zool. Anz., 148:87-93. February.
1952b. Die Amphibien und Reptilien von El Salvador auf grund der reisen von R. Mertens und A. Zilch. Abhand. Senken. Naturw. Gesell., 487:83, 1 Kart., 16 taf. December 1.

MITTLEMAN, M. B.
1944. Feeding habits of a Central American opisthoglyph snake. Copeia, no. 2:122. June 30.

NEILL, W. T. AND ALLEN, R.
1961. Further studies on the herpetology of British Honduras. Herpetologica, 17(1):37-52. April 15.

PARKER, W. K.
1878. On the structure and development of the skull in the common snake *(Tropidonotus natrix)*. Phil. Trans. Roy. Soc. London, pt. 2: 385-417, pp., pls. 27-33.

PETERS, W.
1860. Drei neue amerikanisches Schlangen. Monatsb. Akad. Wiss. Berlin, 1860:517-521, pl., fig. 3. October.

RADOVANOVIC, M.
1937. Osteologie des Schlangenkopfs. Jenaische Zeitschr. Naturw., 71(2):179-312.

SAVAGE, J. M.
1949. Notes on the Central American snake, *Conophis lineatus dunni* Smith, with a record from Honduras. Trans. Kansas Acad. Sci., 50:483-486. December 31.

SCHMIDT, K. P.
1928. Reptiles collected in Salvador for the California Institute of Technology. Zool. Ser. Field Mus. Nat. Hist., 12(16):193-201. November 21.

SCHMIDT, K. P. and INGER, R. F.
1957. Living Reptiles of the World. Garden City, New York, Hanover House. 287 pp.

SMITH, H. M.
1941. Notes on snakes of the genus *Conophis*. Journ. Washington Acad. Sci., 31(3):117-124. March 15.

SMITH, H. M. and TAYLOR, E. H.
1950. Type localities of Méxican reptiles and amphibians. Univ. Kansas Sci. Bull., 33:313-380. March 20.

STUART, L. C.
1948. The amphibians and reptiles of Alta Verapaz, Guatemala. Misc. Publ. Mus. Zool. Univ. Michigan, 69:1-109. June 12.
1954a. A description of a subhumid corridor across northern Central America, with comments on its hertetofaunal indicators. Contr. Lab. Vert. Biol. Univ. Michigan, 65:1-26 pp., 6 pls. March.
1954b. Herpetofauna of the southeast highlands of Guatemala. Contr. Lab. Vert. Biol. Univ. Michigan, 68:1-65 pp., 3 pls. November.

SZUNYOGHY, J.
1932. Beitrage zur vergleichenden Formenlehre des Colubridenschadels, nebst einer Kraniologischen Synopsis der fossilen Schlangen Ungarns. Acta Zool., 13:1-56.

TAYLOR, E. H.
1955. Additions to the known herpetological fauna of Costa Rica with comments on other species. No. II. Univ. Kansas Sci. Bull., 37:299-575. October 15.

TAYLOR, E. H. and SMITH, H. M.
1939. Miscellaneous notes on Mexican snakes. Univ. Kansas Sci. Bull., 25:239-258. July 10.

WETTSTEIN, O.
1934. Ergibnisse der osterreichischen biologischen Costa Rica—Expedition 1930. Die Amphibia und Reptilien. Stiz. Akad. Wiss. Wien, mathem-naturw. kl., Abt. 1, bd. 143:1-39.

Transmitted November 30, 1962.

29-5936

(Continued from inside of front cover)

18. Conspecificity of two pocket mice, Perognathus goldmani and P. artus. By E. Raymond Hall and Marilyn Bailey Ogilvie. Pp. 513-518, 1 map. January 14, 1960.
19. Records of harvest mice, Reithrodontomys, from Central America, with description of a new subspecies from Nicaragua. By Sydney Anderson and J. Knox Jones, Jr. Pp. 519-529. January 14, 1960.
20. Small carnivores from San Josecito Cave (Pleistocene), Nuevo León, México. By E. Raymond Hall. Pp. 531-538, 1 figure in text. January 14, 1960.
21. Pleistocene pocket gophers from San Josecito Cave, Nuevo León, México. By Robert J. Russell. Pp. 539-548, 1 figure in text. January 14, 1960.
22. Review of the insectivores of Korea. By J. Knox Jones, Jr., and David H. Johnson. Pp. 549-578. February 23, 1960.
23. Speciation and evolution of the pygmy mice, genus Baimoys. By Robert L. Packard. Pp. 579-670, 4 plates, 12 figures in text. June 16, 1960.

Index. Pp. 671-690

Vol. 10. 1. Studies of birds killed in nocturnal migration. By Harrison B. Tordoff and Robert M. Mengel. Pp. 1-44, 6 figures in text, 2 tables. September 12, 1956.
2. Comparative breeding behavior of Ammospiza caudacuta and A. maritima. By Glen E. Woolfenden. Pp. 45-75, 6 plates, 1 figure. December 20, 1956.
3. The forest habitat of the University of Kansas Natural History Reservation. By Henry S. Fitch and Ronald R. McGregor. Pp. 77-127, 2 plates, 7 figures in text, 4 tables. December 31, 1956.
4. Aspects of reproduction and development in the prairie vole (Microtus ochrogaster). By Henry S. Fitch. Pp. 129-161, 8 figures in text, 4 tables. December 19, 1957.
5. Birds found on the Arctic slope of northern Alaska. By James W. Bee. Pp. 163-211, plates 9-10, 1 figure in text. March 12, 1958.
*6. The wood rats of Colorado: distribution and ecology. By Robert B. Finley, Jr. Pp. 213-552, 34 plates, 8 figures in text, 35 tables. November 7, 1958.
7. Home ranges and movements of the eastern cottontail in Kansas. By Donald W. Janes. Pp. 553-572, 4 plates, 3 figures in text. May 4, 1959.
8. Natural history of the salamander, Aneides hardyi. By Richard F. Johnston and Gerhard A. Schad. Pp. 573-585. October 8, 1959.
9. A new subspecies of lizard, Cnemidophorus sacki, from Michoacán, México. By William E. Duellman. Pp. 587-598, 2 figures in text. May 2, 1960.
10. A taxonomic study of the middle American snake, Pituophis deppei. By William E. Duellman. Pp. 599-610, 1 plate, 1 figure in text. May 2, 1960.

Index. Pp. 611-626.

Vol. 11. Nos. 1-10 and index. Pp. 1-703, 1958-1960.

Vol. 12. 1. Functional morphology of three bats: Sumops, Myotis, Macrotus. By Terry A. Vaughan. Pp. 1-153, 4 plates, 24 figures in text. July 8, 1959.
*2. The ancestry of modern Amphibia: a review of the evidence. By Theodore H. Eaton, Jr. Pp. 155-180, 10 figures in text. July 10, 1959.
3. The baculum in microtine rodents. By Sydney Anderson. Pp. 181-216, 49 figures in text. February 19, 1960.
*4. A new order of fishlike Amphibia from the Pennsylvanian of Kansas. By Theodore H. Eaton, Jr., and Peggy Lou Stewart. Pp. 217-240, 12 figures in text. May 2, 1960.
5. Natural history of the bell vireo. By Jon C. Barlow. Pp. 241-296, 6 figures in text. March 7, 1962.
6. Two new pelycosaurs from the lower Permian of Oklahoma. By Richard C. Fox. Pp. 297-307, 6 figures in text. May 21, 1962.
7. Vertebrates from the barrier island of Tamaulipas, México. By Robert K. Selander, Richard F. Johnston, B. J. Wilks, and Gerald G. Raun. Pp. 309-345, pls. 5-8. June 18, 1962.
8. Teeth of Edestid sharks. By Theodore H. Eaton, Jr. Pp. 347-362, 10 figures in text. October 1, 1962.

More numbers will appear in volume 12.

Vol. 13. 1. Five natural hybrid combinations in minnows (Cyprinidae). By Frank B. Cross and W. L. Minckley. Pp. 1-18. June 1, 1960.
2. A distributional study of the amphibians of the Isthmus of Tehuantepec, México. By William E. Duellman. Pp. 19-72, pls. 1-8, 3 figures in text. August 16, 1960.
3. A new subspecies of the slider turtle (Pseudemys scripta) from Coahulia, México. By John M. Legler. Pp. 73-84, pls. 9-12, 3 figures in text. August 16, 1960.
4. Autecology of the copperhead. By Henry S. Fitch. Pp. 85-288, pls. 13-20, 26 figures in text. November 30, 1960.
5. Occurrence of the garter snake, Thamnophis sirtalis, in the Great Plains and Rocky Mountains. By Henry S. Fitch and T. Paul Maslin. Pp. 289-308, 4 figures in text. February 10, 1961.
6. Fishes of the Wakarusa river in Kansas. By James E. Deacon and Artie L. Metcalf. Pp. 309-322, 1 figure in text. February 10, 1961.
7. Geographic variation in the North American cyprinid fish, Hybopsis gracilis. By Leonard J. Olund and Frank B. Cross. Pp. 323-348, pls. 21-24, 2 figures in text. February 10, 1961.

(Continued on outside of back cover)

(Continued from inside of back cover)

8. Decriptions of two species of frogs, genus Ptychohyla; studies of American hylid frogs, V. By William E. Duellman. Pp. 349-357, pl. 25, 2 figures in text. April 27, 1961.
9. Fish populations, following a drought, in the Neosho and Marais des Cygnes rivers of Kansas. By James Everett Deacon. Pp. 359-427, pls. 26-30, 3 figs. August 11, 1961.
10. Recent soft-shelled turtles of North America (family Trionychidae). By Robert G. Webb. Pp. 429-611, pls. 31-54, 24 figures in text. February 16, 1962.

Index. Pp. 613-624.

Vol. 14. 1. Neotropical bats from western México. By Sydney Anderson. Pp. 1-8. October 24, 1960.
2. Geographic variation in the harvest mouse. Reithrodontomys megalotis, on the central Great Plains and in adjacent regions. By J. Knox Jones, Jr., and B. Mursaloglu. Pp. 9-27, 1 figure in text. July 24, 1961.
3. Mammals of Mesa Verde National Park, Colorado. By Sydney Anderson. Pp. 29-67, pls. 1 and 2, 3 figures in text. July 24, 1961.
4. A new subspecies of the black myotis (bat) from eastern Mexico. By E. Raymond Hall anad Ticul Alvarez. Pp. 69-72, 1 figure in text. December 29, 1961.
5. North American yellow bats, "Dasypterus," and a list of the named kinds of the genus Lasiurus Gray. By E. Raymond Hall and J. Knox Jones, Jr. Pp. 73-98, 4 figures in text. December 29, 1961.
6. Natural history of the brush mouse (Peromyscus boylii) in Kansas with description of a new subspecies. By Charles A. Long. Pp. 99-111, 1 figure in text. December 29, 1961.
7. Taxonomic status of some mice of the Peromyscus boylii group in eastern Mexico, with description of a new subspecies. By Ticul Alvarez. Pp. 113-120, 1 figure in text. December 29, 1961.
8. A new subspecies of ground squirrel (Spermophilus spilosoma) from Tamaulipas, Mexico. By Ticul Alvarez. Pp. 121-124. March 7, 1962.
9. Taxonomic status of the free-tailed bat, Tadarida yucatanica Miller. By J. Knox Jones, Jr., and Ticul Alvarez. Pp. 125-133, 1 figure in text. March 7, 1962.
10. A new doglike carnivore, genus Cynaretus, from the Clarendonian Pliocene, of Texas. By E. Raymond Hall and Walter W. Dalquest. Pp. 135-138, 2 figures in text. April 30, 1962.
11. A new subspecies of wood rat (Neotoma) from northeastern Mexico. By Ticul Alvarez. Pp. 139-143. April 30, 1962.
12. Noteworthy mammals from Sinaloa, Mexico. By J. Knox Jones, Jr., Ticul Alvarez, and M. Raymond Lee. Pp. 145-159, 1 figure in text. May 18, 1962.
13. A new bat (Myotis) from Mexico. By E. Raymond Hall. Pp. 161-164, 1 figure in text. May 21, 1962.
14. The mammals of Veracruz. By E. Raymond Hall anad Walter W. Dalquest. Pp. 165-362, 2 figures. May 20, 1963.
15. The recent mammals of Tamaulipas, México. By Ticul Alvarez. Pp. 363-473, 5 figures in text. May 20, 1963.

More numbers will appear in volume 14.

Vol. 15. 1. The amphibians and reptiles of Michoacán, México. By William E. Duellman. Pp. 1-148, pls. 1-6, 11 figures in text. December 20, 1961.
2. Some reptiles and amphibians from Korea. By Robert G. Webb, J. Knox Jones, Jr., and George W. Byers. Pp. 149-173. January 31, 1962.
3. A new species of frog (Genus Tomodactylus) from western México. By Robert G. Webb. Pp. 175-181, 1 figure in text. March 7, 1962.
4. Type specimens of amphibians and reptiles in the Museum of Natural History, the University of Kansas. By William E. Duellman and Barbara Berg. Pp. 183-204. October 26, 1962.
5. Amphibians and Reptiles of the Rainforests of Southern El Petén, Guatemala. By William E. Duellman. Pp. 205-249, pls. 7-10, 6 figures in text. October 4, 1963.
6. A revision of snakes of the genus Conophis (Family Colubridae, from Middle America). By John Wellman. Pp. 251-295, 9 figures in text. October 4, 1963.

More numbers will appear in volume 15.

University of Kansas Publications
Museum of Natural History

Volume 15, No. 7, pp. 297-349, pls. 11-18, 7 figs.
October 18, 1963

A Review of the Middle American Tree Frogs of the Genus Ptychohyla

BY

WILLIAM E. DUELLMAN

University of Kansas
Lawrence
1963

UNIVERSITY OF KANSAS PUBLICATIONS
MUSEUM OF NATURAL HISTORY

Institutional libraries interested in publications exchange may obtain this series by addressing the Exchange Librarian, University of Kansas Library, Lawrence, Kansas. Copies for individuals, persons working in a particular field of study, may be obtained by addressing instead the Museum of Natural History, University of Kansas, Lawrence, Kansas. There is no provision for sale of this series by the University Library, which meets institutional requests, or by the Museum of Natural History, which meets the requests of individuals. Nevertheless, when individuals request copies from the Museum, 25 cents should be included, for each separate number that is 100 pages or more in length, for the purpose of defraying the costs of wrapping and mailing.

* An asterisk designates those numbers of which the Museum's supply (not the Library's supply) is exhausted. Numbers published to date, in this series, are as follows:

Vol. 1. Nos. 1-26 and index. Pp. 1-638, 1946-1950.

*Vol. 2. (Complete) Mammals of Washington. By Walter W. Dalquest. Pp. 1-444, 140 figures in text. April 9, 1948.

Vol. 3. *1. The avifauna of Micronesia, its origin, evolution, and distribution. By Rollin H. Baker. Pp. 1-359, 16 figures in text. June 12, 1951.
*2. A quantitative study of the nocturnal migration of birds. By George H. Lowery, Jr. Pp. 361-472, 47 figures in text. June 29, 1951.
3. Phylogeny of the waxwings and allied birds. By M. Dale Arvey. Pp. 473-530. 49 figures in text, 13 tables. October 10, 1951.
*4. Birds from the state of Veracruz, Mexico. By George H. Lowery, Jr., and Walter W. Dalquest. Pp. 531-649, 7 figures in text, 2 tables. October 10, 1951.
Index. Pp. 651-681.

*Vol. 4. (Complete) American weasels. By E. Raymond Hall. Pp. 1-466, 41 plates, 31 figures in text. December 27, 1951.

Vol. 5. Nos. 1-37 and index. Pp. 1-676, 1951-1953.

*Vol. 6. (Complete) Mammals of Utah, *taxonomy and distribution*. By Stephen D. Durrant. Pp. 1-549, 91 figures in text, 30 tables. August 10, 1952.

Vol. 7. Nos. 1-15 and index. Pp. 1-651, 1952-1955.

Vol. 8. Nos. 1-10 and index. Pp. 1-675, 1954-1956.

Vol. 9. *1. Speciation of the wandering shrew. By James S. Findley. Pp. 1-68, 18 figures in text. December 10, 1955.
2. Additional records and extension of ranges of mammals from Utah. By Stephen D. Durrant, M. Raymond Lee, and Richard M. Hansen. Pp. 69-80. December 10, 1955.
3. A new long-eared myotis (Myotis evotis) from northeastern Mexico. By Rollin H. Baker and Howard J. Stains. Pp. 81-84. December 10, 1955.
4. Subspeciation in the meadow mouse, Microtus pennsylvanicus, in Wyoming By Sydney Anderson. Pp. 85-104, 2 figures in text. May 10, 1956.
5. The condylarth genus Ellipsodon. By Robert W. Wilson. Pp. 105-116, 6 figures in text. May 19, 1956.
6. Additional remains of the multituberculate genus Eucosmodon. By Robert W. Wilson. Pp. 117-123, 10 figures in text. May 19, 1956.
7. Mammals of Coahuila, Mexico. By Rollin H. Baker. Pp. 125-335, 75 figures in text. June 15, 1956.
8. Comments on the taxonomic status of Apodemus peninsulae, with description of a new subspecies from North China. By J. Knox Jones, Jr. Pp. 337-346, 1 figure in text, 1 table. August 15, 1956.
9. Extensions of known ranges of Mexican bats. By Sydney Anderson. Pp. 347-351. August 15, 1956.
10. A new bat (Genus Leptonycteris) from Coahuila. By Howard J. Stains. Pp. 353-356. January 21, 1957.
11. A new species of pocket gopher (Genus Pappogeomys) from Jalisco, Mexico. By Robert J. Russell. Pp. 357-361. January 21, 1957.
12. Geographic variation in the pocket gopher, Thomomys bottae, in Colorado. By Phillip M. Youngman. Pp. 363-387, 7 figures in text. February 21, 1958.
13. New bog lemming (genus Synaptomys) from Nebraska. By J. Knox Jones, Jr. Pp. 385-388. May 12, 1958.
14. Pleistocene bats from San Josecito Cave, Nuevo León, México. By J. Knox Jones, Jr. Pp. 389-396. December 19, 1958.
15. New subspecies of the rodent Baiomys from Central America. By Robert L. Packard. Pp. 397-404. December 19, 1958.
16. Mammals of the Grand Mesa, Colorado. By Sydney Anderson. Pp. 405-414, 1 figure in text, May 20, 1959.
17. Distribution, variation, and relationships of the montane vole, Microtus montanus. By Sydney Anderson. Pp. 415-511, 12 figures in text, 2 tables. August 1, 1959.

(Continued on inside of back cover)

University of Kansas Publications
Museum of Natural History

Volume 15, No. 7, pp. 297-349, pls. 11-18, 7 figs.
October 18, 1963

A Review of the Middle American Tree Frogs of the Genus Ptychohyla

BY

WILLIAM E. DUELLMAN

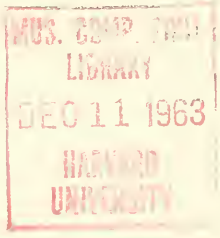
University of Kansas
Lawrence
1963

University of Kansas Publications, Museum of Natural History

Editors: E. Raymond Hall, Chairman, Henry S. Fitch,
Theodore H. Eaton, Jr.

Volume 15, No. 7, pp. 297-349, pls. 11-18, 7 figs.
Published October 18, 1963

University of Kansas
Lawrence, Kansas



PRINTED BY
JEAN M. NEIBARGER, STATE PRINTER
TOPEKA, KANSAS
1963

29-6531

A Review of the Middle American Tree Frogs of the Genus Ptychohyla

BY

WILLIAM E. DUELLMAN

CONTENTS

PAGE

INTRODUCTION 301
Acknowledgments 301
Materials and Methods 302
ANALYSIS OF DATA 303
External Morphology 303
Color and Pattern 307
Osteology 307
Tadpoles 310
Breeding Call 312
SYSTEMATIC ACCOUNTS 314
Ptychohyla Taylor, 1944 314
Key to Adults 315
Key to Tadpoles 315
Ptychohyla euthysanota Group 315
Ptychohyla euthysanota 315
Ptychohyla euthysanota euthysanota (Kellogg) 315
Ptychohyla euthysanota macrotympanum (Tanner) 320
Ptychohyla leonhardschultzei (Ahl) 323
Ptychohyla spinipollex (Schmidt) 327
Ptychohyla schmidtorum Group 331
Ptychohyla schmidtorum 331
Ptychohyla schmidtorum schmidtorum Stuart 331
Ptychohyla schmidtorum chamulae Duellman 334
Ptychohyla ignicolor Duellman 337
DISTRIBUTION AND ECOLOGY 340
Geographic Distribution of the Species 340
Habitat Preference 342
Interspecific Competition 343
Reproduction and Development 344

PAGE
Phylogeny of Ptychohyla 345
Ptychohyla as a Natural Assemblage 345
Generic Relationships 346
Interspecific Relationships 347
Literature Cited 349

INTRODUCTION

Probably no ecological group of hylid frogs (some *Hyla* plus *Plectrohyla* and *Ptychohyla*) in Middle America is so poorly known as those species that live in the cloud forests on steep mountain slopes and breed in cascading mountain streams. During the last half of the nineteenth century most of the species of hylids living in the lowlands of southern México and northern Central America were named and described. Despite the extensive collecting by Salvin and Godman, Nelson and Goldman, and the various expeditions of the *Mission Scientifique*, no members of the genus *Ptychohyla* were obtained until 1927, when in the mountains of El Salvador Ruben A. Stirton found a small tree frog that subsequently was described and named *Hyla euthysanota* by Kellogg (1928). Until recently frogs of this genus were know from few specimens and in the literature by nearly as many names.

Although I first collected *Ptychohyla* in 1956, it was not until 1960 that special efforts were made to obtain specimens of this genus. The summer of 1960 was spent in southern México and Guatemala, where every accessible stream in the cloud forests was searched for tree frogs, especially *Ptychohyla* and *Plectrohyla.* Similar, but less extensive, investigations were carried out in 1961 and 1962. The result of this field work is a rather large collection of *Ptychohyla* representing all of the known species, plus tape recordings of the breeding calls and tadpoles of all of the species.

Previously, I have discussed the nomenclature of one of the species (Duellman, 1960) and have described two new species (Duellman, 1961). In the latter paper I made reference to a future account (this one) that would deal with the systematics and biology of the entire genus. Although I have series of specimens, tadpoles, osteological preparations, and recordings of breeding calls, thereby having a wide array of data at my disposal, much still remains to be learned about these frogs, especially about various aspects of their life histories. Even the validity of the genus is open to question; this problem is discussed at length in the section beyond entitled "*Ptychohyla* as a Natural Assemblage."

Acknowledgments

I am indebted to the following persons for permitting me to examine specimens in their care: Miguel Alvarez del Toro, Museo Zoología de Tuxtla Gutierrez, México (MZTG); Charles M. Bogert and Richard G. Zweifel, American Museum of Natural History (AMNH); Doris M. Cochran, United States

National Museum (USNM); Norman Hartweg and Charles F. Walker, University of Michigan Museum of Zoology (UMMZ); Robert F. Inger, Chicago Natural History Museum (CNHM); Hobart M. Smith, University of Illinois Museum of Natural History (UIMNH); Heinz Wermuth, Zoologisches Museum Berlin (ZMB); and Ernest E. Williams, Museum of Comparative Zoology (MCZ). The abbreviations following names of institutions will be used throughout the text; the Museum of Natural History at the University of Kansas is abbreviated KU.

Throughout my work on these frogs I have profited from discussions with L. C. Stuart, who has made many valuable suggestions and with his characteristic generosity has placed at my disposal his extensive collections of tadpoles from Guatemala. For his aid I am indeed grateful. I am grateful to Thomas E. Moore for tapes of breeding calls of two species.

My own field work was made more enjoyable and profitable through the assistance of Dale L. Hoyt, Craig E. Nelson, Jerome B. Tulecke, and John Wellman, all of whom spent many hours in often unsuccessful attempts to collect specimens and record breeding calls of *Ptychohyla*. I am indebted to many residents of México, Guatemala, and El Salvador for permission to work on their land and for providing shelter, food, and guides. I am especially grateful to Mr. and Mrs. Horatio Kelly of "Colegio Linda Vista" at Pueblo Nuevo Solistahuacán, Chiapas, for a pleasant stay at their school; Jordi Juliá Z. of the Comisión del Papaloapan, Ciudad Alemán, Veracruz, for arranging for field work in northern Oaxaca in 1959; Walter Hannstein and Lothar Menzel for the use of facilities at Finca La Paz, Guatemala, in 1960; Alan Hempstead for the use of facilities at Finca Los Alpes, Guatemala in 1960 and 1961; and Julio Aguirre C. of the Instituto Tropical de Investigaciones Científicas, San Salvador, El Salvador, for providing comfortable working quarters and transportation and guides to the mountains in northern El Salvador. Without the cheerful efforts of Jorge A. Ibarra, Director of the Museo Nacional de Historia Natural in Guatemala, my field work would have been greatly restricted during politically precarious times in that country. Permits to collect in México were furnished by the late Luis Macías Arellano of the Dirección General de Caza. Each of these individuals has my profound thanks for his indispensable aid.

Field work on hylid frogs in Middle America has been supported by the National Science Foundation, Grant NSF-G9827, and this is the 9th publication on the results of study of the material from America.

Materials and Methods

During the course of this study I have examined 247 frogs that I assign to the genus *Ptychohyla*, plus 40 lots of tadpoles and 12 skeletal preparations. Furthermore, I have examined all of the type specimens. I have studied each of the species and subspecies in the field and have examined from seven (*P. euthysanota macrotympanum*) to 33 (*P. spinipollex*) living individuals of each species.

Measurements given in the analysis of data and in the descriptions of the species are those described by Duellman (1956). In the descriptions of living colors the capitalized names are from Ridgway (1912). All interpretations of osteological characters are based on specimens cleared in potassium hydroxide and stained with alizarin red.

Recordings of the breeding calls were made with a Magnemite Portable Tape-recorder; audiospectrographs were made on a vibralyzer (Kay Electric Company) using normal pattern and wide bandwidth.

ANALYSIS OF DATA

Data that are used to arrive at a systematic arrangement of the species of *Ptychohyla* are analyzed and discussed below for the values inherent in the analysis. These data are of some value also in the recognition of species and subspecies but if employed for that purpose the data must be used in combination with the keys and the diagnoses of the individual species and subspecies.

External Morphology

Each of the external morphological characters used in the systematic treatment of *Ptychohyla,* as well as the nature of the tongue, is discussed below.

SIZE AND PROPORTIONS.—Comparisons of size and certain proportions are given in Table 1. Frogs of this genus are small; the largest specimen examined is a female of *P. euthysanota euthysanota* having a snout-vent length of 53.3 mm. The species comprising the *Ptychohyla schmidtorum* group are smaller; the largest specimen examined is a female of *P. schmidtorum schmidtorum* having a snout-vent length of 38.0 mm. An analysis of the various measurements and proportions shows few constant differences. *Ptychohyla ignicolor* differs from all of the other species in having the head slightly wider than long and the tympanum noticeably less than half the size of eye. *Ptychohyla spinipollex* has a relatively narrow interorbital distance, approximately equal to the width of the eyelid, whereas in all of the other species that distance is much more than the width of the eyelid.

SNOUT.—All species have a blunt snout. In *P. leonhardschultzei* and *P. ignicolor* the snout is nearly square in lateral profile; in *P. schmidtorum* the snout is slightly rounded above and below, and in the other species it is rounded above. *Ptychohyla leonhardschultzei* and *P. spinipollex* have a vertical fleshy rostral keel on the snout; in these speces, because of this keel, the snout in dorsal profile is pointed. The nostrils are slightly protuberant in all species, and in *P. schmidtorum* the internarial region is slightly depressed.

HAND.—The species in the *Ptychohyla euthysanota* group have a vestige of web between the first and second fingers; the other fingers are about one-third webbed. Breeding males have a cluster of horny nuptial spines on the thumb. The spines are largest in *P.*

TABLE 1.—VARIATION IN CERTAIN CHARACTERS IN THE SPECIES OF PTYCHOHYLA. (MEANS ARE IN PARENTHESES BELOW THE RANGES.)

Species	Sex	Number of specimens	Maximum snout-vent length	Tibia length / Snout-vent length	Tympanum / Eye	Vomerine teeth
P. euthysanota euthysanota	♂	17	38.1	44.4–55.0 (48.7)	48.6–63.8 (56.3)	4–6 (5.1)
	♀	15	53.3	46.5–56.6 (51.4)	42.9–56.4 (51.4)	6–18 (9.6)
P. euthysanota macrotympanum	♂	5	38.0	48.8–52.0 (50.2)	50.0–57.1 (54.1)	0–4 (2.6)
	♀	5	44.8	46.4–54.1 (50.2)	48.7–58.9 (53.7)	8–10 (9.2)
P. leonhardschultzei	♂	16	35.6	48.8–56.1 (51.2)	48.7–61.9 (52.1)	6–9 (6.5)
	♀	3	41.6	52.3–59.5 (54.7)	47.5–48.6 (48.1)	7–12 (9.5)
P. spinipollex	♂	32	41.2	46.9–53.1 (49.0)	45.0–55.2 (49.5)	3–7 (4.9)
	♀	6	44.6	46.1–50.2 (48.8)	47.7–53.8 (50.4)	6–10 (7.6)
P. schmidtorum schmidtorum	♂	25	32.8	45.3–52.4 (48.1)	51.5–59.3 (54.7)	5–11 (6.2)
	♀	9	38.0	46.5–49.1 (47.7)	51.3–58.3 (54.9)	7–11 (8.7)
P. schmidtorum chamulae	♂	40	30.5	46.0–51.9 (48.2)	48.2–65.6 (54.9)	4–6 (4.7)
	♀	4	31.8	48.1–52.4 (50.5)	51.4–61.7 (55.7)	4–9 (6.2)
P. ignicolor	♂	13	30.5	45.9–52.2 (49.6)	37.1–47.1 (43.2)	3–9 (6.1)

spinipollex (Fig. 1) and vary in number from 35 to 66 (average 47.4) on each thumb. In the other species of the *Ptychohyla euthysanota* group the spines are smaller and usually more numerous; the numbers of spines on each thumb (means in parentheses) in members of this group are: *P. euthysanota euthysanota,* 44-143 (83.8); *P. euthysanota macrotympanum,* 40-110 (63.0); *P. leonhard-*

schultzei, 24-80 (54.7). The species in the *Ptychohyla schmidtorum* group have no web between the first and second fingers and only a vestige of web between the other fingers. Furthermore, these species lack nuptial spines in breeding males. Like the usual horny excresences on the thumbs of many species of frogs, the horny spines on the thumbs of members of the *Ptychohyla euthysanota* group are seasonal in development.

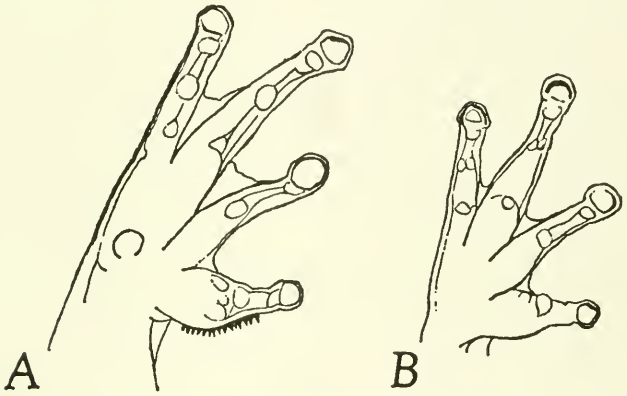


FIG. 1. Palmar views of right hands of (A) *Ptychohyla spinipollex* (KU 58054) and (B) *Ptychohyla schmidtorum schmidtorum* (KU 58043). × 4.

Many workers have used the presence of a bifid subarticular tubercle beneath the fourth finger as a diagnostic character of certain species of hylids. Examination of the subarticular tubercles in *Ptychohyla* reveals considerable intraspecific variation. Bifid tubercles beneath the fourth finger are found in all species except *P. ignicolor,* which is known from only two specimens. In *P. euthysanota euthysanota* nearly 60 per cent and in *P. schmidtorum schmidtorum* about 90 per cent of the specimens have a bifid tubercle beneath the fourth finger on one or both hands. All specimens of *P. leonhardschultzei* have either a bifid or double tubercle beneath the fourth finger, and some have a bifid distal tubercle beneath the third finger.

FEET.—Members of the *Ptychohyla euthysanota* group have a weak tarsal fold, whereas in the species comprising the *Ptychohyla schmidtorum* group the tarsal fold is absent. Webbing on the foot extends to the discs of the third and fifth toes and to the base of the penultimate phalanx of the fourth toe, except in *P. ignicolor,* which has less webbing.

VENTROLATERAL GLANDS.—Breeding males develop thickened, pigmented glandular areas on the sides of the body. In living specimens of *P. schmidtorum* and *P. ignicolor* the glands are not readily visible, but in preservative they show as distinctive orange-colored areas. These glands are most distinct in *P. euthysanota;* in many specimens of this species the glands are elevated above the surrounding skin. The extent of the glands is variable (Fig. 2); probably this variability is due to different degrees of development in individual frogs rather than to interspecific differences. All *Ptychohyla ignicolor* and some *P. schmidtorum chamulae* have a small, round glandular area on the chin; to my knowledge this does not occur in the other species. Superficial examination of microscopic preparations of the glands reveals no histological differences between species. The glands occupy most of the thickened area and have narrow ducts leading to the exterior. Detailed studies of the histology will be reported elsewhere. Since the glands are developed only in breeding males, it is surmised that the glands are associated with some phase of the breeding activity.

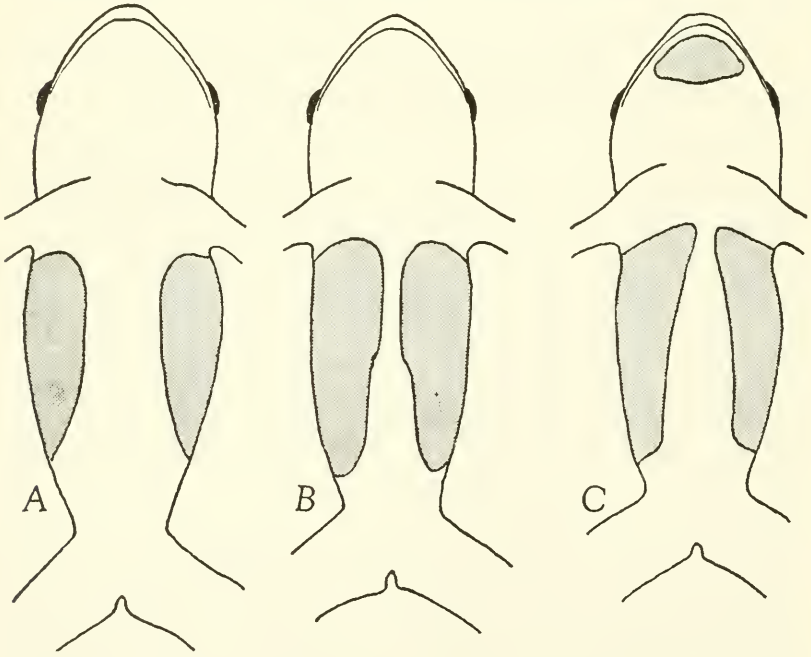


FIG. 2. Normal extent of ventrolateral glands in (A) *Ptychohyla euthysanota euthysanota* (KU 58008), (B) *Ptychohyla schmidtorum schmidtorum* (KU 58037), and (C) *Ptychohyla ignicolor* (UMMZ 119603). × 2¼.

Tongue.—The shape of the tongue varies intraspecifically. Usually the tongue is ovoid; in some specimens it is barely notched posteriorly, whereas in others it is deeply notched, making the tongue cordiform. Deeply notched cordiform tongues are found in *P. leonhardschultzei* and *P. schmidtorum;* with the exception of these two species, some individuals of all species have emarginate tongues. Some individuals of all species have tongues that are shallowly notched posteriorly.

Color and Pattern

The dorsum in living frogs of the genus *Ptychohyla* is primarily yellowish or reddish brown, except in *P. schmidtorum chamulae* and *P. ignicolor* in which it is green. Usually there are some darker blotches or reticulations on the dorsum. The venter usually is white; in *P. ignicolor* it is yellow. The venter is spotted in all members of the *Ptychohyla euthysanota* group; the species, arranged from least to most spotting ventrally, are: *P. euthysanota euthysanota, P. euthysanota macrotympanum, P. leonhardschultzei,* and *P. spinipollex.* The last two species also have bold dark spots on the flanks. *Ptychohyla schmidtorum* lacks spots on the venter, whereas *P. ignicolor* has small dark flecks ventrally.

Ptychohyla euthysanota and *P. schmidtorum* have white stripes on the upper lips and on the flanks. All species have some form of a pale stripe above the anus and usually rather distinct white or pale stripes along the ventrolateral edges of the tarsi and forearms. There are no bright or boldly marked flash-colors (colors that are revealed only when the hind limbs are extended), except in *P. ignicolor,* which has bright red flash-colors in the groin and on the thighs. In life the iris varies from several different shades of bronze color to deep red in *P. schmidtorum schmidtorum.*

The degree of metachrosis is moderate. Usually any change of color in life consists only of change in the intensity of color. At times when the over-all coloration is darkened some markings are obscured.

Osteology

The following description of the skull, hyoid, sternum, and prepollex is based on a male specimen of *P. spinipollex* (KU 68632) that has been cleared and stained. The broad, flat skull (Fig. 3) has a large frontoparietal fontanelle. The ethmoid is large and has a flange laterally. The nasals are of moderate size and in broad contact with the ethmoid, but are separated from one another

medially. The anterior half of the maxillary bears a thin, high flange. The anterior process of the squamosal is short and widely separated from the maxillary. The quadratojugal is a small spine-shaped element projecting anteriorly from the ventral base of the quadrate; the quadratojugal does not articulate with the maxillary.

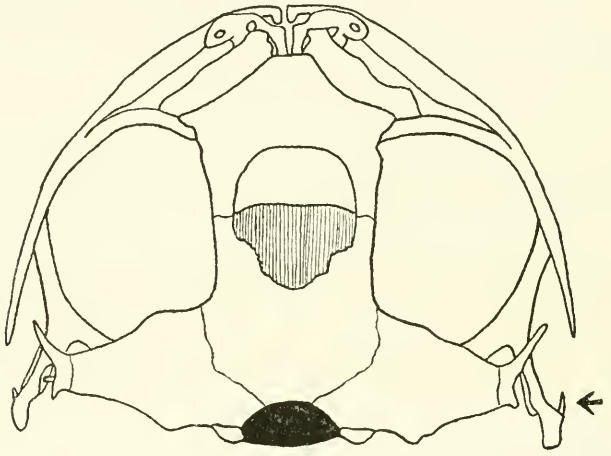


Fig. 3. Dorsal aspect of skull of *Ptychohyla spinipollex* (KU 68632). Arrow indicates reduced quadratojugal. × 6.

The posteromedian part of the hyoid plate is calcified; from this plate the long bony, posterior cornua (thyrohyales) extend posterolaterally.

The omosternum is calcified, widest anteriorly, and has a convex anterior edge. The calcified xiphisternum is roughly bell-shaped having short lateral processes anteriorly and a deep notch posteriorly.

The swollen thumb is supported by a dorsoventrally flattened spine that does not extrude through the skin.

Variation.—In general, the skull varies little. Usually the quadratojugal is present only as a short element attached to the quadrate, but in one specimen of *P. spinipollex* the quadratojugal articulates with the maxillary and forms a complete quadratojugal-maxillary arch on each side of the skull. One specimen of *P. leonhardschultzei* has a complete arch on one side and an incomplete arch on the other.

Only *P. spinipollex* has lateral processes anteriorly on the xiphisternum; in the other species the xiphisterum is deeply bell-shaped.

Ptychohyla schmidtorum and *P. ignicolor* have slightly longer

premaxillaries than the other species. The longer premaxillary is reflected in the larger number of teeth on the bone—9 to 11 (average 10) in four specimens of *P. schmidtorum* and 10 teeth in one *P. ignicolor,* as compared with 6 to 10 (average 7.9) in seven specimens of the other species. The number of maxillary teeth in the various species are: *P. euthysanota euthysanota,* 43; *P. euthysanota macrotympanum,* 38; *P. leonhardschultzei,* 38 and 40; *P. spinipollex,* 34 and 40; *P. schmidtorum schmidtorum,* 37 and 43; *P. schmidtorum chamulae,* 40 and 41; *P. ignicolor,* 43. The teeth on the premaxillary and anterior part of the maxillary are long, pointed, and terminally curved backwards. Posteriorly on the maxillary the teeth become progressively shorter and blunter.

Variation in number of vomerine teeth is shown in Table 1.

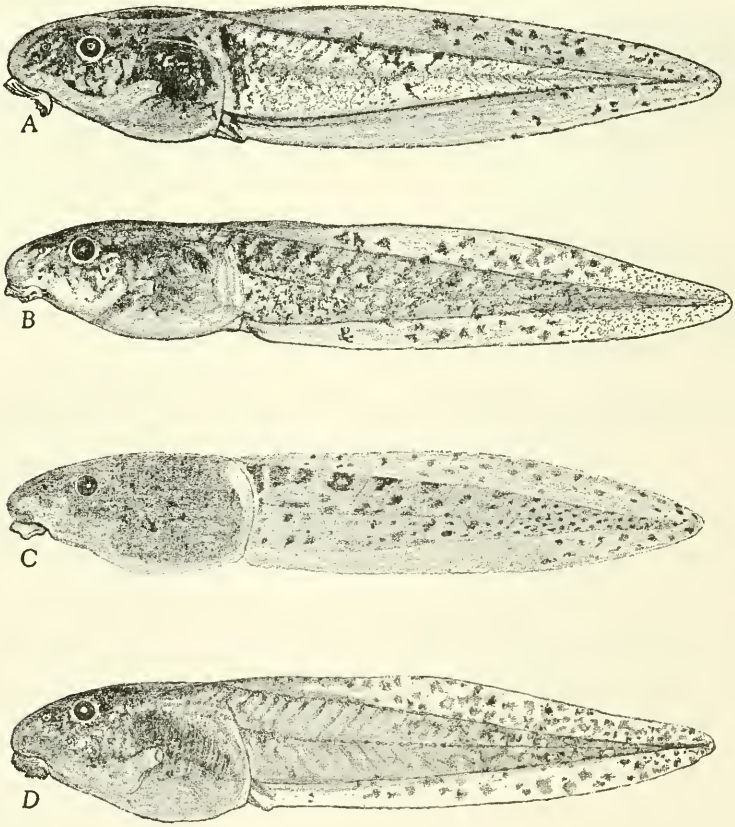


FIG. 4. Tadpoles of the *Ptychohyla euthysanota* group: (A) *P. euthysanota euthysanota* (KU 60042), (B) *P. euthysanota macrotympanum* (KU 60049), (C) *P. leonhardschultzei* (KU 68556), and (D) *P. spinipollex* (KU 60053). ×2½.

Tadpoles

Tadpoles of the genus *Ptychohyla* are adapted to live in mountain streams. The bodies are streamlined, and the tails are long and have low fins (Figs. 4 and 5). The mouths are large and directed ventrally. Tadpoles of the two groups of species have strikingly different mouthparts.

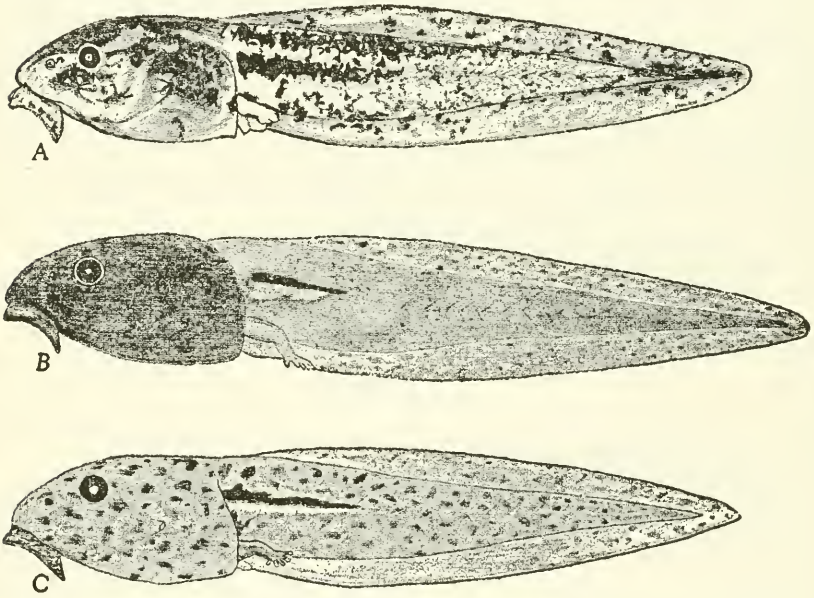


Fig. 5. Tadpoles of (A) *Ptychohyla schmidtorum schmidtorum* (KU 60051), (B) *P. schmidtorum chamulae* (KU 58199), and (C) *P. ignicolor* (KU 71716). × 2½.

Lips of tadpoles of the *Ptychohyla euthysanota* group (Fig. 6 A-D) are folded laterally; there are ⅙ or sometimes ⅐ tooth-rows. A lateral "wing" projects on either side of the upper beak. The beaks have blunt, peglike serrations. Lips of tadpoles of the *Ptychohyla schmidtorum* group (Fig. 6 E-G) are greatly expanded and form a funnel-shaped disc; there are ⅔ short tooth-rows. There is no lateral projection or "wing" on either side of the upper beak. The beaks have long, pointed serrations.

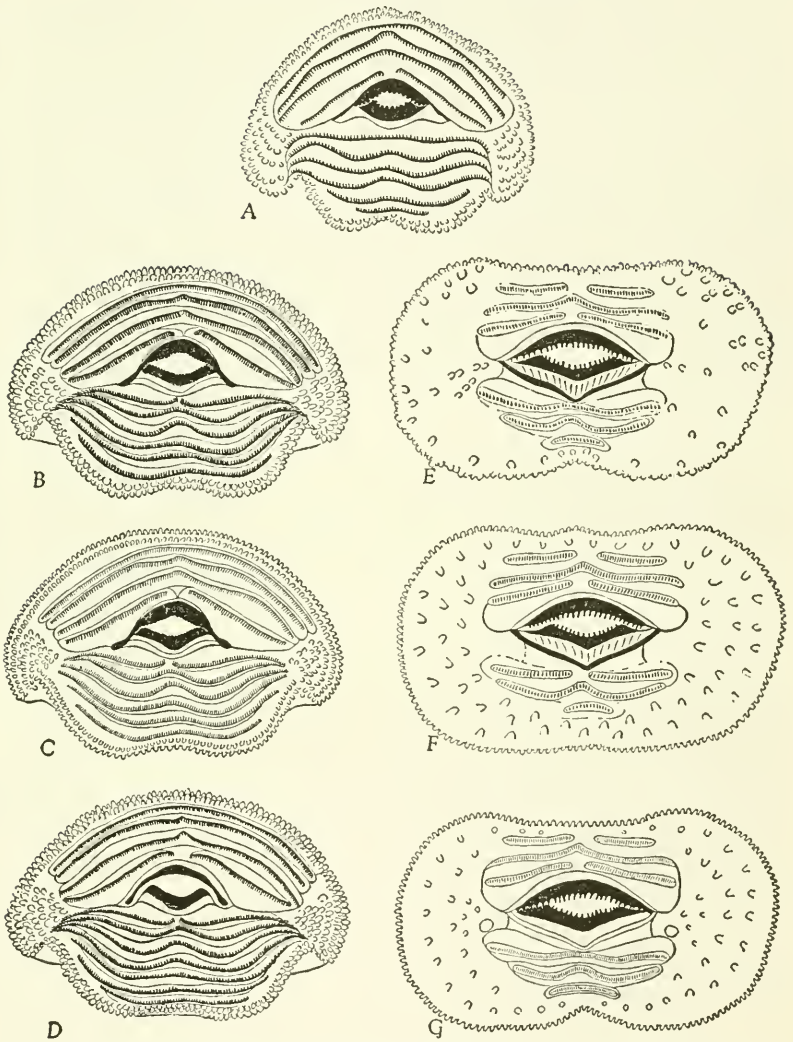


FIG. 6. Mouthparts of tadpoles of *Ptychohyla*: (A) *P. euthysanota euthysanota* (KU 60042), (B) *P. euthysanota macrotympanum* (KU 60049), (C) *P. leonhardschultzei* (KU 68556), (D) *P. spinipollex* (KU 60053), (E) *P. schmidtorum schmidtorum* (KU 60051), (F) *P. schmidtorum chamulae* (KU 58199), and (G) *P. ignicolor* (KU 71716). × 10.

Variation in certain structural details and in coloration is discussed for each species and subspecies in the systematic accounts that follow. Sizes, proportions, and numbers of tooth-rows are tabulated in Table 2.

TABLE 2.—COMPARISON OF CERTAIN LARVAL CHARACTERS IN THE SPECIES OF PTYCHOHYLA. (MEANS ARE IN PARENTHESES BELOW THE RANGES.)

Species	Number of specimens	Maximum total length	Head length / Total length	Tooth-rows
P. euthysanota euthysanota	23	40.8	30.9–37.3 (33.5)	4/6
P. euthysanota macrotympanum	13	43.3	30.6–33.4 (32.7)	4/6
P. leonhardschultzei	7	47.5	29.2–32.7 (31.1)	4/6
P. spinipollex	32	45.0	30.2–35.9 (33.0)	4/7
P. schmidtorum schmidtorum	14	42.5	28.9–31.2 (29.9)	3/3
P. schmidtorum chamulae	4	45.0	26.9–29.3 (27.8)	3/3
P. ignicolor	2	39.6	29.6–29.8 (29.7)	3/3

Evidence on the pattern of development of tooth-rows indicates that the inner rows develop first. A small tadpole of *P. euthysanota euthysanota* has six lower rows and three fully developed upper rows and only the beginning of the first (outer) upper row. A small tadpole of *P. euthysanota macrotympanum* has four upper rows and five lower rows. In a small tadpole of *P. leonhardschultzei* the three upper and four lower tooth-rows are well developed; the first upper and fifth lower rows are beginning to develop, and the sixth lower row is absent. In small tadpoles of *P. spinipollex*, the sixth lower row is poorly developed, and the seventh row is absent; large individuals normally have seven lower rows. A small tadpole of *P. schmidtorum chamulae* has ⅗ tooth-rows.

Breeding Call

Breeding calls of all species and subspecies of *Ptychohyla* were recorded in the field. Obtaining series of calls of *Ptychohyla* is difficult because these frogs call mostly from vegetation along roaring mountain streams and only by locating a calling frog some distance from the water or along a quiet stretch of the stream can good recordings be obtained. For example, four individuals of

P. spinipollex were recorded, but only one recording was sufficiently free of background noise to be analyzed.

Analysis of breeding calls supports the division of the genus *Ptychohyla* into two groups of species. The call of each member of the *Ptychohyla euthysanota* group consists of a single long note, whereas the call of species in the *Ptychohyla schmidtorum* group consists of a series of short notes. Since no differences were found between the calls of subspecies of any given species, the following discussion of breeding calls pertains to species. These calls are described briefly below and at greater length in the systematic accounts farther on. Audiospectrographs of the breeding calls are shown in Plate 1, and comparisons of the characteristics of the calls are given in Table 3.

TABLE 3.—COMPARISON OF THE BREEDING CALLS OF PTYCHOHYLA

Species	Number	Notes per call group	Duration of note (seconds)	Pulses per second	Frequency range (cps)	Dominant frequency (cps)
P. spinipollex	1	1	.46	147	3000–5100	4300
P. euthysanota	7	1	.62 (.60–.65)	95.3 (91–102)	1800–4200	3070 (3000–3200)
P. leonhardschultzei	2	1	.79 (.62–.95)	77 (76–78)	1500–3500	2750 (2700–2800)
P. schmidtorum	6	8.5* (8–9)	.064 (.054–.070)	110 (96–121)	1400–5800	3400 (3350–3450)
P ignicolor	2	12* (11–13)	.079 (.078–.080)	126 (123–129)	1000–5000	3150 (3100–3200)

*Only an analysis of the long series of calls is given here; see text for explanation.

P. spinipollex (Pl. 1 A).—One long note is repeated at intervals of 45 seconds to four minutes and has an average dominant frequency of 4300 cycles per second.

P. euthysanota (Pl. 1 B).—One long note is repeated six to nine times at intervals of 2.7 to 3.4 seconds and has an average dominant frequency of 3070 cycles per second.

P. leonhardschultzei (Pl. 1 C).—One long note is repeated once after 10 to 13 seconds and has an average dominant frequency of 2750 cycles per second.

P. schmidtorum (Pl. 1 D).—The complete call consists of one short series of notes alternating with two long series. Numbers of notes per series in one individual having a typical call were 5-8-8-3-9-9. The average dominant frequency of notes in the short and long series alike is 3400 cycles per second.

P. ignicolor (Pl. 1 E).—The complete call consists of a short series of notes alternating with a long series. In one complete recording the numbers of notes in these series were 4-13-3-11. The notes in the short series have an average dominant frequency of 2100 cycles per second, whereas the notes in

the long series have an average dominant frequency of 3150 cycles per second. The four series of notes were given in one minute and 15 seconds.

SYSTEMATIC ACCOUNTS

The museum catalogue numbers of the specimens examined, together with the localities from which they came, are listed at the end of the account of each subspecies or monotypic species. The localities that are represented by symbols on the distribution map (Fig. 7) are in roman type; those that are not represented on the map, because overlapping of symbols would have occurred, are in italic type.

Ptychohyla Taylor, 1944

Ptychohyla Taylor, Univ. Kansas Sci. Bull., 30:41, May 15, 1944. Type, *Ptychohyla adipoventris* Taylor, 1944 [= *Hyla leonhardschultzei* (Ahl), 1934].

Diagnosis.—Small hylids having stream-adapted tadpoles and differing from other hylid genera in having large ventrolateral glands in breeding males.

Composition.—Five species, two of which are made up of two subspecies, arranged in two groups of species on the basis of morphological characters of adults and tadpoles and on the basis of breeding calls.

Distribution.—Moderate elevations from southern Guerrero and northern Oaxaca, México, to northern El Salvador and central Honduras.

Key to Adults

1. A weak tarsal fold; outer fingers one-third webbed; males having spiny nuptial tuberosities; color in life tan or brown with blotches or reticulations, never green; iris bronze color ..... *P. euthysanota* group—2

   No tarsal fold; outer fingers having only vestige of web; males lacking nuptial tuberosities; color in life green or brown; iris red or golden color ..... *P. schmidtorum* group—5

2. Chest, throat, and flanks usually having brown or black spots; no distinct white stripe on upper lip or on flanks; a faint white line usually present above anal opening; a rostral keel 3

   Chest, throat, and flanks usually unspotted; distinct white line on upper lip and on flank present or not; white line above anal opening faint or well defined; no rostral keel 4

3. Interorbital region much wider than eyelid; spots on throat and chest black; spots only occasionally present on belly; flanks marbled with black and white; nuptial spines small, as many as 80 on one thumb ..... *P. leonhardschultzei*

   Interorbital region about as wide as eyelid; spots on chest and throat brown or black; spots usually present on belly; flanks having round brown or black spots; nuptial spines moderate in size, conical, seldom more than 60 on one thumb ..... *P. spinipollex*

4. A distinct, broad, white lateral stripe usually present; usually a distinct white line above anal opening; a distinct white stripe on upper lip ..... *P. euthysanota euthysanota*

   No white lateral stripe; a faint white stripe above anal opening; no distinct white stripe on upper lip ..... *P. euthysanota macrotympanum*

5. A distinct, broad, lateral stripe; a white stripe on upper lip expanded to form a large spot below eye; hidden surfaces of thighs and webs of

feet not red in life; internarial region slightly depressed; diameter of tympanum greater than one-half diameter of eye 6

No lateral white stripe; no stripe on upper lip; in life dorsum green, hidden surfaces of thighs and webs of feet orange tan to bright red, and eye golden color; internarial region flat; diameter of tympanum less than one-half diameter of eye ..... *P. ignicolor*

6. Webs of feet and posterior surfaces of thighs pale cream color; dorsum in life reddish brown; iris bright red ..... *P. schmidtorum schmidtorum*

Webs of feet and posterior surfaces of thighs pale brown; dorsum in life green; iris reddish bronze color ..... *P. schmidtorum chamulae*

KEY TO TADPOLES

1. Lips greatly expanded forming a funnel-shaped mouth; tooth-rows ⅔ ..... *P. schmidtorum* group—2

Lips folded laterally, not forming a funnel-shaped mouth; tooth-rows ⅙ or more ..... *P. euthysanota* group—4

2. Belly and mouth mottled; tail cream color heavily blotched with brown 3

Belly dark gray; tail cream color with dense brown flecking, giving brown appearance ..... *P. schmidtorum chamulae*

3. Belly cream color with brown mottling; no large tubercle at each end of first lower tooth-row ..... *P. schmidtorum schmidtorum*

Belly grayish green with brown mottling; a large tubercle at each end of first lower tooth-row ..... *P. ignicolor*

4. Tooth-rows ⅙; cream-colored crescent-shaped mark on posterior part of body bordered posteriorly by large brown mark 5

Tooth-rows usually ⅐ (sometimes ⅙); cream-colored crescent-shaped mark on posterior part of body usually indistinct, not bordered posteriorly by large brown mark ..... *P. spinipollex*

5. Caudal musculature uniformly flecked with brown; lower tooth-rows 1-4 about equal in length to upper rows ..... *P. euthysanota euthysanota*

Caudal musculature having brown square blotches dorsally on anterior one-half of tail; lower tooth-rows 1-4 usually slightly shorter than upper rows 6

6. Dorsal caudal blotches well defined and extending onto sides of tail; moderately large brown flecks on caudal fin; eye in life pale reddish brown ..... *P. leonhardschultzei*

Dorsal caudal blotches faint, not extending onto sides of tail; small brown flecks on caudal fin; eye in life silvery bronze ..... *P. euthysanota macrotympanum*

The *Ptychohyla euthysanota* Group

Three species in group; adults having moderate amount of webbing between fingers, and tarsal fold; breeding males having spinous, horny, nuptial tuberosities on pollex; mouths of tadpoles having lateral folds in lips and ⅙ or ⅐ tooth-rows; breeding call consisting of one long note.

Ptychohyla euthysanota

Diagnosis.—Rostral keel absent; nuptial spines in males small; interorbital region much wider than eyelid.

Ptychohyla euthysanota euthysanota (Kellogg)

Hyla euthysanota Kellogg, Proc. Biol. Soc. Washington, 41:123-124, June 29, 1928 [Holotype.—USNM 73296 from Los Esemiles, Depto. Chalatenango, El Salvador; Ruben A. Stirton collector]. Mertens, Sencken-

bergiana, 33:169-171, June 15, 1952; Abhand. Senckenbergische Naturf. Gesell., 487:29, December 1, 1952. Stuart, Proc. Biol. Soc. Washington, 67:169, August 5, 1954.

Hyla rozellae Taylor, Univ. Kansas Sci. Bull., 28:78-80, pl. 9, fig. 1, May 15, 1942 [Holotype.—USNM 115039 from Salto de Agua, Chiapas, México; Hobart M. and Rozella Smith collectors]. Taylor and Smith, Proc. U. S. Natl. Mus., 95:587, June 30, 1945. Smith and Taylor, Bull. U. S. Natl. Mus., 194:86, June 17, 1948. Stuart, Proc. Biol. Soc. Washington, 67:169, August 5, 1954.

Ptychohyla bogerti Taylor, Amer. Mus. Novitates, 1437:13-16, fig. 5, December 7, 1949 [Holotype.—AMNH 51847 from Río Grande, Oaxaca, México; Thomas MacDougall collector]. Stuart, Proc. Biol. Soc. Washington, 67:169, August 5, 1954.

Ptychohyla euthysanota, Duellman, Univ. Kansas Publ. Mus. Nat. Hist., 13:351, April 27, 1961.

Diagnosis.—Dorsum tan to reddish brown; venter white; rarely flecked with brown or black; a white stripe on upper lip, on flank, and usually above anus.

Description.—The following description is based on KU 58008 from Finca La Paz, Depto. San Marcos, Guatemala (Pl. 2). Adult male having a snout-vent length of 35.0 mm.; tibia length, 16.5 mm.; tibia length/snout-vent length, 47.1 per cent; foot length, 14.2 mm.; head length, 11.0 mm.; head length/snout-vent length, 31.4 per cent; head width, 10.7 mm.; head with/snout-vent length, 30.6 per cent; diameter of eye, 3.3 mm.; diameter of tympanum, 1.8 mm.; tympanum/eye, 54.5 per cent. Snout in lateral profile nearly square, slightly rounded above, and in dorsal profile bluntly rounded; canthus pronounced; loreal region moderately concave; lips thick, rounded, and slightly flaring; nostrils protuberant; internarial distance, 3.0 mm.; top of head flat; interorbital distance, 4.1 mm., and approximately a third broader than width of eyelid, 2.9 mm. Moderately heavy dermal fold from posterior corner of eye above tympanum to point above insertion of forelimb, covering upper edge of tympanum; tympanum round, its diameter slightly more than its distance from eye. Forearm moderately robust, having distinct dermal fold on wrist; dermal fold, but no row of tubercles along ventrolateral surface of forearm; pollex only slightly enlarged, bearing triangular shaped patch of small horn-covered spines (128 on right, 134 on left); second and fourth fingers equal in length; subarticular tubercles round, distal one on fourth finger bifid; discs moderate in size, that of third finger equal to diameter of tympanum; no web between first and second fingers; other fingers one-third webbed. Heels broadly overlap when hind limbs adpressed; tibiotarsal articulation reaches to middle of eye; low rounded tarsal fold; inner metatarsal tubercle large, elliptical, and flat; outer metatarsal tubercle small and round; low dermal fold from heel to disc of fifth toe; subarticular tubercles round; length of digits from shortest to longest 1-2-5-3-4; third and fifth toes webbed to base of disc; fourth toe webbed to proximal end of penultimate phalanx; thin dermal fold from inner metatarsal tubercle to disc of first toe; disc smaller than on fingers. Anal opening at the level of the upper edge of thighs; anal flap short; anal opening bordered above by thin transverse dermal fold and laterally by heavy dermal fold. Skin of dorsum and ventral surfaces of forelimbs and shanks smooth; that of throat, belly, and ventral surfaces of thighs granular. Ventrolateral glands moderately developed, not reaching axilla or groin and broadly separated midventrally. Tongue ovoid, emarginate, and only slightly free posteriorly; vomerine teeth 2-2, situated on small triangular elevations between ovoid inner nares; openings

to vocal sac large, one situated along inner posterior edge of each mandibular ramus.

Dorsal ground-color of head, body, and limbs dull reddish brown with irregular dark brown reticulations on head and body and dark brown transverse bands on limbs; dorsal surfaces of first and second fingers and webbing on hand cream color; dorsal surfaces of third and fourth fingers dull brown; anterior surfaces of thighs dull creamy yellow; posterior surfaces of thighs dull brown; tarsi and toes tan with brown flecks; webbing of feet brown; faint creamy white stripe along lateral edges of tarsi and forearms; thin white line along edge of upper lip; distinct white stripe above and beside anal opening; axilla white; throat, chest, belly, and ventral surfaces of forelimbs creamy white; flanks white, separated from pale venter by a row of partly connected dark brown spots; ventral surfaces of thighs dull creamy yellow; feet grayish brown; ventrolateral glands pale grayish brown; small brown flecks on periphery of chin.

In life the dorsal ground-color was pale reddish brown (Orange-Cinnamon); dorsal reticulations dark brown (Chocolate); dorsal surfaces of first and second fingers and webbing on hands creamy tan (Light Pinkish Cinnamon); posterior surfaces of thighs reddish brown (Vinaceous-Tawny); webbing of feet gray (Deep Mouse Gray); throat and belly grayish white (Pale Gull Gray); ventral surfaces of hind limbs creamy white (Marguerite Yellow); spots on flanks dark brown (Warm Sepia); iris reddish bronze (Apricot Orange).

Variation.—No geographic variation in structural characters is discernible; variation in size and proportions is given in Table 1. Of 32 adults examined, seven have the tongue shallowly notched posteriorly; in the others the tongue is emarginate. Twenty specimens have a bifid subarticular tubercle beneath the fourth finger; in the others there are no bifid tubercles.

The coloration described above is typical of the 16 specimens available from Finca La Paz. The living coloration at night, when the frogs were collected, was somewhat darker than the living colors described above, which were recorded for the frogs the morning after collection, at which time one individual had a pale reddish brown dorsum (Orange-Cinnamon) with dull olive green (Deep Grape Green) reticulations on the back and transverse bands on the limbs; the dorsal surfaces of the first and second fingers and the discs on the third and fourth fingers were orange (Mikado Orange).

More than half of the specimens from Finca La Paz agree in all essential characters with the description given above. The distinctness of the white stripe on the upper lip is variable; in two individuals the stripe is barely discernible. Likewise, in some individuals the white stripe on the flanks is not distinct, either because there are few or no brown spots separating the stripe from the pale venter, or because the ventrolateral gland has diffused the pale color on the flanks. There is some noticeable variation in dorsal coloration, either through a greater or lesser development of dark pigment. One specimen (KU 58007) is grayish tan above with dark brown markings; the posterior surfaces of the thighs are dull grayish yellow; the first and second fingers and the webbing on the hands are pale yellowish gray; the belly and throat are dusty white; the flecks on the throat are gray; the ventral surfaces of the feet are grayish brown. Dark individuals, such as KU 58009 have a uniform dark brownish black dorsum; the belly is cream; the first and second

fingers and the webbing on the hands are dull creamy tan; the dorsal and ventral surfaces of the feet are dark brown. In KU 58013 there is a heavy suffusion of brown on the throat and flanks. Two specimens have scattered white flecks on the dorsum.

The reddish brown dorsal ground-color with dark brown reticulations on the head and body and dark brown transverse bands on the limbs seems to be rather constant throughout the range of the subspecies. Likewise, the presence of the white stripe on the upper lip and the white stripe around the anal opening are present on most specimens. In breeding males having well-developed ventrolateral glands the lateral white stripe often is obliterated.

Description of Tadpole.—The following description is based on KU 60042 from Finca La Paz, Depto. San Marcos, Guatemala (Figs. 4A and 6A). No limb buds; total length, 35.8 mm.; body length, 11.2 mm.; body length/total length, 31.3 per cent. Body moderately depressed, slightly wider than deep, ovoid in dorsal profile; mouth directed ventrally; eyes small, directed dorsolaterally; nostrils slightly protuberant and directed anteriorly, closer to eye than snout; spiracle sinistral and posteroventrad to eye; anal tube dextral. Caudal fin low, rounded posteriorly; depth of caudal musculature about one-half greatest depth of caudal fin; musculature extends nearly to tip of tail.

Mouth large; lips having deep lateral folds; two complete rows of papillae on lips; five to six rows of papillae laterally. Beaks moderately developed, bearing peglike serrations; slender lateral projections on upper beak; tooth-rows 4/6; upper rows subequal in length, second longest; fourth row interrupted medially; lower rows complete; lower rows 1-4 equal in length to upper rows; fifth lower row somewhat shorter; sixth lower row short.

Body brown above; tip of snout cream color; grayish cream color below; caudal musculature creamy tan; caudal fin transparent; cream-colored crescent-shaped mark on posterior edge of body and anterior part of caudal musculature, bordered posteriorly by dark brown blotch; scattered brown flecks on caudal musculature and posterior part of caudal fin. Eye bronze color in life.

Variation.—The variation in size and proportions is given in Table 2. In some specimens the first upper tooth-row is irregular, sometimes broken, and often shorter than other upper tooth-rows. Usually the fourth upper and first lower, and sometimes the sixth lower, tooth-rows are interrupted medially. One specimen has a short, irregular, seventh lower tooth-row; all others have six.

The cream-colored crescent-shaped mark usually is distinct. The brown blotch posterior to this mark is variously shaped ranging from a narrow vertical bar to a triangular blotch. Brown flecks seldom are present on the anterior part of the ventral caudal fin.

Comparisons.—Aside from the characters given in the diagnosis, *P. euthysanota euthysanota* can be distinguished from both *P. spinipollex* and *P. leonhardschultzei* by the absence of bold black and white marbling on the flanks; furthermore, from the former it can be distinguished by having more and smaller horny nuptial spines and from the latter by having the snout, in lateral profile, rounded above and not acutely angulate. *Ptychohyla euthysanota euthysanota* differs from *P. euthysanota macrotympanum* by normally having a darker dorsal color, broader stripe on upper lip, and a distinct lateral stripe.

Occurring sympatrically with *Ptychohyla euthysanota euthysanota* are several species of *Plectrohyla*, all of which differ in having a bony prepollex, rather

rugose skin on the dorsum, and more squat bodies. Other sympatric species are *Ptychohyla schmidtorum schmidtorum,* which lacks a tarsal fold and nuptial spines and has a red eye in life, *Hyla salvadorensis,* which has a green dorsum and lacks spinous nuptial tuberosities, and *Hyla sumichrasti,* a small yellow frog usually lacking vomerine teeth.

Life History.—This subspecies breeds in clear, swift mountain streams. Males call from stems and leaves of plants at the edge of, or overhanging, the streams. The breeding call consists of a soft "wraack," repeated at intervals of three to four seconds. Each note has a duration of 0.60 to 0.65 seconds and has 91 to 102 pulses per second; the dominant frequency falls between 3000 and 3200 cycles per second.

Tadpoles in various stages of development were found at Finca La Paz, Guatemala, in late July. This indicates that there is either extreme differential growth, or, more probably, an extended breeding season. A tadpole having a body length of 6.8 mm. and a total length of 19.1 mm. has a short median first upper tooth-row; lower tooth-rows 3-6 are only two-thirds as long as lower rows 1 and 2. Two recently metamorphosed young have snout-vent lengths of 14.2 and 14.8 mm.; they are colored like the adults.

Remarks. — The type specimen of *Hyla euthysanota* Kellogg (1928:123) is a female; therefore, when Taylor (1944) proposed the name *Ptychohyla* for hylids having ventrolateral glands in breeding males, he was unaware that *Hyla euthysanota* was a member of this group. In his description of *Hyla rozellae,* Taylor (1942) did not compare his specimens with *Hyla euthysanota,* but instead placed *H. rozellae* with *H. loquax* and *H. rickardsi.* The type series of *H. rozellae* consists of one large adult female and several metamorphosing young. Taylor (1949:16) based the description of *Ptychohyla bogerti* on two males and compared these specimens with *P. adipoventris* Taylor [= *P. leonhardschultzei* (Ahl)]. Thus, in a period of 22 years the females of this species were given two names and the male another. Stuart (1954:169) suggested that *Hyla euthysanota* and *Hyla rozellae* were *Ptychohyla.* Now that sufficient specimens are available from throughout the range it is possible to determine that the various named populations are conspecific.

Distribution.—This subspecies inhabits cloud forests at elevations of 660 to 2200 meters on the Pacific slopes of the Sierra Madre from extreme eastern Oaxaca and western Chiapas, México, through Guatemala to northern El Salvador; probably it occurs also in southwestern Honduras. Aside from the specimens listed below, three in the Frankfurt Museum from Depto. Santa Ana, El Salvador (44571, Hacienda San José; 43040, Hacienda Los Planes; 65119, Miramundo) are listed by Mertens (1952:29).

Specimens examined.—Mexico: *Chiapas: Cascarada, 30 km. W of Ciltapec,* UMMZ 87851-2; Cerro Ovando, UMMZ 87853-4; Chicomuselo, UMMZ 94439-40; Finca Juárez, 28 km. N of Escuintla, USNM 115052-5; *Las Nubes, Cerro Ovando,* USNM 115030-8; Salto de Agua, USNM 115039-51. *Oaxaca:* Cerro Pecho Blanco, UIMNH 40963; between La Gloria and Cerro Azul, UIMNH 40976-7; Río Grande, AMNH 51847-8; Santo Tomás Tecpan, UIMNH 41071.

Guatemala: *San Marcos:* Finca La Paz, 2 km. W of La Reforma, KU 58001-14, 59937 (skeleton), 60042-3 (tadpoles), 60044 (4 young), MCZ 34997, UMMZ 107739, 123151-7 (tadpoles); Finca Pirineos, Río Samalá, CNHM 35066. *Santa Rosa:* Finca La Gloria, UMMZ 123148 (tadpoles), 123150 (tadpoles). *Sololá:* Finca Santo Tomás, UMMZ 123149 (tadpoles); Olas de Mocá, near Mocá, CNHM 20208.

El Salvador: *Chalatenango:* Los Esemiles, USNM 73296. *Santa Ana:* Miramundo, CNHM 65120.

Ptychohyla euthysanota macrotympanum (Tanner)

Hyla macrotympanum Tanner, Great Basin Nat., 17:52-53, July 31, 1957 [Holotype.—AMNH 62141 (formerly BYU 13752) from 10 miles east of Chiapa de Corzo, Chiapas, México; Robert Bohlman collector].

Ptychohyla macrotympanum, Duellman, Univ. Kansas Publ. Mus. Nat. Hist., 13:351, April 27, 1961.

Diagnosis.—Dorsum usually pale tan; venter white with scattered brown or black flecks; a thin white stripe on upper lip and another above anal opening; no distinct white stripe on flanks.

Description.—The following description is based on KU 58049 from Linda Vista, Chiapas, México (Pl. 3). Adult male having a snout-vent length of 38.0 mm.; tibia length, 19.5 mm.; tibia length/snout-vent length, 51.3 per cent; foot length, 15.7 mm.; head length, 11.8 mm.; head length/snout-vent length, 31.1 per cent; head width, 11.7 mm.; head width/snout-vent length, 30.8 per cent; diameter of eye, 3.8 mm.; diameter of tympanum, 2.1 mm.; tympanum/eye, 55.2 per cent. Snout in lateral profile nearly square, slightly rounded above, and in dorsal profile bluntly rounded; canthus pronounced; loreal region concave; lips thick, rounded, and slightly flaring; nostrils protuberant; internarial distance, 3.1 mm.; top of head flat; interorbital distance, 3.8 mm., and approximately a fourth broader than width of eyelid, 3.1 mm. A moderately heavy dermal fold from posterior corner of eye above tympanum to point above insertion of forelimb, covering upper edge of tympanum; tympanum round, its diameter equal to its distance from eye. Forearm moderately robust, having a distinct dermal fold on wrist; dermal fold, but no row of tubercles along ventrolateral surface of forearm; pollex only slightly enlarged, bearing triangular patch of small horn covered spines (94 on right, 100 on left); fourth finger slightly longer than second; subarticular tubercles round, none bifid; discs moderate in size, that of third finger equal to diameter of tympanum; vestige of web between first and second fingers; other fingers one-third webbed. Heels broadly overlap when hind limbs adpressed; tibiotarsal articulation reaches to middle of eye; weak tarsal fold on distal two-thirds of tarsus; inner metatarsal tubercle large, elliptical, and flat; outer metatarsal tubercle small and round; no dermal fold from heel to disc of fifth toe; subarticular tubercles round; length of digits from shortest to longest 1-2-5-3-4; third toe webbed to base of disc; fifth toe webbed to middle of penultimate phalanx; fourth toe webbed to proximal end of penultimate phalanx; no fold of skin from inner metatarsal tubercle to base of disc on first

toe; discs much smaller than on fingers. Anal opening near upper edge of thighs; short anal flap bordered above by thin dermal fold; small tubercles and heavy dermal fold lateral to anal opening. Skin of dorsum and ventral surfaces of fore limbs and shanks smooth; that of throat, belly, and ventral surfaces of thighs granular. Ventrolateral glands weakly developed, not reaching axilla or groin and broadly separated midventrally. Tongue ovoid, shallowly notched posteriorly, and barely free behind; vomerine teeth 2-2, situated on small triangular elevations between ovoid inner nares; openings to vocal sac large, one situated along inner posterior edge of each mandibular ramus.

Dorsal ground-color of head, body, and limbs pale pinkish tan with the greatest part of head and body covered by large gray interconnected blotches; black flecks over most of dorsum; grayish brown transverse bands on shanks; dorsal surfaces of first and second fingers pale grayish yellow; dorsal surfaces of third and fourth fingers and webbing on hand pale grayish tan; anterior surfaces of thighs pale flesh-color; posterior surfaces of thighs pale grayish yellow; dorsal surfaces of tarsi and toes pale grayish tan with black flecks; webbing of feet pale gray; faint creamy white stripes along ventrolateral edges of tarsi and forearms; a very thin white line along edge of upper lip; a narrow grayish white stripe above anal opening; axilla gray; throat, chest, belly, and ventral surfaces of forelimbs pale grayish white; ventral surfaces of hind limbs cream color; flanks gray flecked with brown; ventral surfaces of feet grayish tan; ventrolateral glands pinkish tan; anterior one-half of chin flecked with brown.

In life the dorsum was pale tan (Pinkish Buff); the dark markings on dorsum dull brown (Tawny-Olive); tarsi pale tan (Pale Pinkish Buff); flanks pinkish tan (Pale Cinnamon-Pink); iris coppery bronze (Capucine Orange).

Variation.—The few specimens from a limited geographic region preclude any analysis of geographic variation. All specimens, except the one described above, have the fifth toe webbed to the base of the disc. Many individuals have a bifid subarticular tubercle beneath the fourth finger. The shape of the posterior edge of the tongue varies from nearly straight and shallowly notched to bluntly rounded and emarginate. Two females (KU 58050-1) have more pointed snouts in dorsal profile than do males.

Some specimens, such as KU 58048, are notably darker than the specimen described above; in dark specimens the dorsum is brown with dark brown markings; all fingers and the webbing on the hand are brown. The tarsi and feet are like those in the specimen described above, but the posterior surfaces of the thighs are yellowish tan heavily suffused with brown; the venter is cream color. In life KU 58048 had a brown (Verona Brown) dorsum with dark brown (Chocolate) markings. KU 58047 is slightly darker than KU 58048 and has scattered small white flecks on the dorsum. All specimens have the thin white line on the upper lip, but in some individuals it is indistinct. The grayish white line above the anus is present in all specimens.

Description of Tadpole.—The following description is based on KU 60049 from Río Hondo, 9.5 kilometers south of Pueblo Nuevo Solistahuacán, Chiapas, México (Figs. 4B and 6B). No limb buds; total length, 36.2 mm.; body length, 11.1 mm.; body length/total length, 30.6 per cent. Body moderately depressed, slightly wider than deep, ovoid in dorsal profile; mouth directed ventrally; eyes small, directed dorsolaterally; nostrils slightly protuberant and

directed anteriorly, somewhat closer to eye than snout; spiracle sinistral and posteroventrad to eye; anal tube dextral. Caudal fin low, acutely rounded posteriorly; depth of caudal musculature slightly more than one-half greatest depth of caudal fin; caudal musculature extending nearly to tip of tail.

Mouth large; lips having deep lateral folds; two complete rows of papillae on lips; five or six rows of papillae laterally. Beaks moderately developed, bearing small peglike serrations; moderately wide lateral projections on upper beak; tooth-rows 4/6; upper rows subequal in length; fourth row interrupted medially; length of lower rows 1-4 subequal to upper rows; fifth and sixth lower rows decreasing in length; first lower row interrupted medially.

Body brown above; tip of snout cream color; venter creamy white; caudal musculature creamy tan; caudal fin transparent; cream-colored crescent-shaped mark on posterior edge of body and anterior part of caudal musculature, bordered posterodorsally by dark brown blotch; four dark brown blotches on dorsum of anterior part of caudal musculature; scattered brown flecks on caudal musculature and fin; eye silvery bronze in life.

Variation.—The variation in size and proportions is given in Table 2. All specimens have 4/6 tooth-rows; in some the first lower row is interrupted medially. Specimens from Jacaltenango and two kilometers west of San Pedro Necta, Depto. Huehuetenango, Guatemala, have weakly developed sixth lower tooth-rows.

The cream-colored crescent-shaped mark is distinct in all specimens; the dorsal blotches on the anterior part of the caudal musculature are narrow and do not extend far onto the sides of the tail. The blotches are most distinct in small tadpoles and sometimes indistinct in large ones.

Comparisons.—*Ptychohyla euthysanota macrotympanum* can be distinguished from both *P. spinipollex* and *P. leonhardschultzei* by the absence of bold black and white marbling on the flanks, as well as by the characters given in the diagnosis; furthermore, from the former it differs in having more and smaller horny nuptial tuberosities and from the latter by having the snout, in lateral profile, rounded above instead of angulate. *Ptychohyla euthysanota macrotympanum* differs from *P. e. euthysanota* by normally having a paler dorsum, narrower stripe on upper lip, and no distinct lateral stripe.

Ptychohyla euthysanota macrotympanum occurs sympatrically with *Plectrohyla guatemalensis* and *P. matudai matudai.* Each of the last two has a bony prepollex, rather rugose skin on the dorsum, and more squat body. Other sympatric species are *Hyla walkeri,* which has a green dorsum with brown markings and a rather pointed snout, and *Hyla sumichrasti,* a small yellow frog usually lacking vomerine teeth.

Life History.—This species breeds in clear mountain streams in mixed pine and broad-leafed forest. Males call from trees and bushes along the streams. The breeding call consists of a soft "wraack," repeated three to nine times with intervals of 2.7 to 3.4 seconds between notes. Each note has a duration of 0.60 to 0.65 second, and a rate of 92 to 100 pulses per second; the dominant frequency falls between 3000 and 3200 cycles per second (Pl. 1B). The call is indistinguishable from that of *P. e. euthysanota.*

Tadpoles in various stages of development were found in the Río Hondo, Chiapas, on June 16, 1960. The smallest tadpole has a total length of 24.1 mm.; in this individual the sixth lower tooth row has barely started to develop. A metamorphosing frog taken at the same time has a snout-vent length of 19.8 mm., a short remnant of the tail, and the mouth and tongue developed, whereas another individual having a snout-vent length of 17.8 mm. and a tail 31.0 mm. in length still has larval teeth. Three completely metamorphosed juveniles collected by L. C. Stuart at Jacaltenango, Guatemala, on June 6 and 7, 1955, have snout-vent lengths of 16.0, 16.0, and 16.1 mm.

Remarks.—Tanner (1957:52) based the description of *Hyla macrotympanum* on a single female, which, of course, lacked the characters diagnostic of *Ptychohyla.* On the basis of general external characters Tanner suggested that *Hyla macrotympanum* was related to *H. miotympanum,* from which it differed in having a larger tympanum and a bifid subarticular tubercle beneath the fourth finger. The collection of additional females, together with males of the species, has shown that *Hyla macrotympanum* is a *Ptychohyla.*

Intergradation between *Ptychohyla euthysanota* and *P. macrotympanum* has not been demonstrated. Currently their ranges are separated by the dry valleys of the Río Grijalva and Río Cuilco. The similarity in structure of the adults and tadpoles and the indistinguishable breeding calls are the basis for considering the two populations subspecies.

Distribution.—This species occurs in mixed pine and broad-leafed forests at elevations of 700 to 1700 meters on the southern slopes of the Chiapan Highlands and Sierra de Cuchumatanes, in Guatemala. These forests are on the south facing slopes north of the valleys of the Río Grijalva and Río Cuilco.

Specimens examined.—Mexico: *Chiapas:* 6 km. NE of Chiapa de Corzo, TCWC 16183; 16 km. E of Chiapa de Corzo, AMNH 62141; Linda Vista, 2 km. NW of Pueblo Nuevo Solistahuacán, KU 58049-51, 59939 (skeleton); *Río Hondo, 9.5 km. S of Pueblo Nuevo Solistahuacán,* KU 58047-8, 60046-7, 60048-9 (tadpoles); San Fernando, MZTG 15, 17; Tonina (ruins), KU 41592.

Guatemala: *Huehuetenango:* Jacaltenango, UMMZ 123139 (tadpoles); 0.5 km. E of Jacaltenango, UMMZ 123142-3; 2 km. S of Jacaltenango, UMMZ 123141; 2 km. W of San Pedro Necta, UMMZ 123140 (tadpoles).

Ptychohyla leonhardschultzei (Ahl)

Hyla leonhard-schultzei Ahl, Zool. Anz., 106:185-186, fig. 1, April 15, 1934 [Holotype.—ZMB 34353 from Malinaltepec, Guerrero, México; Leonhard Schultze collector]. Smith and Taylor, Bull. U. S. Natl. Mus., 184:87, June 17, 1948.

Hyla godmani, Ahl, Zool. Anz., 106:186, April 15, 1934.

Hyla pinorum Taylor, Proc. Biol. Soc. Washington, 50:46-48, pl. 2, fig. 2,

April 21, 1937 [Holotype.—UIMNH 25049 from Agua del Obispo, Guerrero, México; Edward H. Taylor collector]. Smith and Taylor, Bull. U. S. Natl. Mus., 194:87, June 17, 1948.

Ptychohyla adipoventris Taylor, Univ. Kansas Sci. Bull., 30:41-45, May 15, 1944 [Holotype.—UIMNH 25047 from Agua del Obispo, Guerrero, México; Edward T. Taylor collector]. Smith and Taylor, Bull. U. S. Natl. Mus., 194:91, June 17, 1948. Taylor, Amer. Mus. Novitates, 1437:16, December 7, 1949. Stuart, Proc. Biol. Soc. Washington, 67:169, August 5, 1954.

Hyla milleri Shannon, Proc. U. S. Natl. Mus., 101:473-477, figs. 92b, 93a-c, May 17, 1951 [Holotype.—USNM 123700 from San Lucas Camotlán, Oaxaca, México; Walter S. Miller collector].

Ptychohyla leonhard-schultzei, Duellman, Herpetologica, 16:191-197, figs. 1-3, September 23, 1960; Univ. Kansas Publ. Mus. Nat. Hist., 13:351, April 27, 1961.

Diagnosis.—Rostral keel present; snout in lateral profile not rounded above; interorbital region much broader than eyelid; distal subarticular tubercle beneath fourth finger bifid or double; no white stripe on edge of upper lip; flanks white with black spots.

Description.—The following description is based on KU 64117 from Vista Hermosa, Oaxaca, México (Pl. 4). Adult male having a snout-vent length of 35.6 mm.; tibia length, 18.0 mm.; tibia length/snout-vent length, 50.5 per cent; foot length, 14.3 mm.; head length, 10.7 mm.; head length/snout-vent length, 30.1 per cent; head width, 10.6 mm.; head width/snout-vent length, 29.8 per cent; diameter of eye, 3.6 mm.; diameter of tympanum, 1.8 mm.; tympanum/eye, 50.0 per cent. Snout in lateral profile square, not rounded above, and in dorsal profile rounded with pointed tip resulting from vertical rostral keel; canthus pronounced; loreal region barely concave; lips thick, rounded, and barely flaring; nostrils protuberant; internarial distance, 3.2 mm.; top of head flat; interorbital distance, 3.8 mm., and approximately a fifth broader than width of eyelid, 3.2 mm. A moderately heavy dermal fold from posterior corner of eye above tympanum and curving ventrad to anterior edge of insertion of forelimb, covering upper edge of tympanum; tympanum round, its diameter equal to its distance from eye. Forearm moderately robust, having distinct dermal fold on wrist; row of small, low, rounded tubercles along ventrolateral surface of forearm; pollex only slightly enlarged, bearing triangular patch of small horn-covered spines (56 on right, 62 on left); second finger noticeably shorter than fourth; subarticular tubercles round, distal ones on third and fourth toes bifid; discs moderate in size, that of third finger slightly larger than diameter of tympanum; no web between first and second fingers; other fingers one-third webbed. Heels broadly overlap when hind limbs adpressed; tibiotarsal articulation reaches to middle of eye; a low rounded tarsal fold on distal half of tarsus; inner metatarsal tubercle elevated, flat, and elliptical; outer metatarsal tubercle at base of fourth toe, round; row of low, sometimes indistinct, tubercles from heel to base of fifth toe; subarticular tubercles round; length of digits from shortest to longest 1-2-3-5-4, third and fifth being about equal in length; third and fifth toes webbed to base of disc; fourth toe webbed to base of penultimate phalanx; discs of toes much smaller than on fingers. Anal opening near dorsal surface of thighs; short anal flap; opening bordered laterally by heavy dermal fold and ventrolaterally by large tubercles. Skin of dorsum and ventral surfaces of forelimbs and shanks smooth; that of throat, belly, and ventral surfaces of thighs granular. Ventrolateral glands

moderately developed, reaching axilla but not to groin and broadly separated midventrally. Tongue cordiform, shallowly notched behind and barely free posteriorly; vomerine teeth 4-3, situated on transverse elevations between ovoid inner nares; openings to vocal sac large, one situated along inner posterior edge of each mandibular ramus.

Dorsal ground-color of head, body, and limbs pale tan with large interconnected dark brown blotches on head and body and broad dark brown transverse bands on limbs; dorsal surfaces of first and second fingers and of webbing of hands pale brown; dorsal surfaces of third and fourth fingers dark brown; anterior surfaces of thighs flesh-color; posterior surfaces of thighs brown; dorsal surfaces of tarsi and feet dark brown; narrow white stripe along ventrolateral edges of forearms and tarsi; a faint creamy white stripe above anal opening; axilla white; flanks creamy white, boldly spotted with black; throat and chest white; ventral surfaces of tarsi and feet dark brown; other ventral surfaces dusty cream color; large brown spots on chin and anterior part of abdomen.

In life the dorsum was reddish brown (Orange-Cinnamon) with dark brown (Chocolate) blotches; first and second fingers and webbing on hand pale reddish brown (Cinnamon); webbing on feet dark brown (Clove Brown); flanks pale creamy white (Pale Olive Buff) with dark brown (Bone Brown) spots; iris reddish bronze (Apricot Orange).

Variation.—No noticeable geographic variation is apparent in the few available specimens; variations in proportions are given in Table 1. The distal subarticular tubercle of the fourth finger is either bifid or double in all specimens; that on the third finger usually is bifid, sometimes single. The vertical rostral keel is prominent in all freshly preserved specimens; in some older specimens it is indistinct. The tongue always is notched posteriorly; in some individuals the notch is shallow; in others it is deep.

Some specimens are paler and less boldly marked than the specimen described above. All specimens from Agua del Obispo and some specimens from the northern slopes of the Sierra Madre Oriental in Oaxaca have a pale tan dorsum with brown markings. In most individuals the white color in the axilla extends onto the posterior edge of the upper arm. The creamy white color of the flanks is constant and usually extends slightly dorsad in the inguinal region. The white stripe above, and sometimes continuing down beside, the anal opening varies from a thin indistinct line or row of flecks to a distinct continuous stripe. Two specimens have dark brown spots on the belly; in the others the spots are confined to the flanks and throat.

Description of tadpole.—The following description is based on KU 68556 from 7.5 kilometers south of Yetla, Oaxaca, México (Figs. 4C and 6C). No limb buds; total length, 37.3 mm.; body length, 12.2 mm.; body length/total length, 32.7 per cent; body slightly depressed, barely wider than deep, ovoid in dorsal profile; mouth directed ventrally; eyes small, directed dorsolaterally; nostrils barely protuberant and directed anterolaterally, about midway between snout and eye; spiracle sinistral and posteroventrad to eye; anal tube dextral. Caudal fin low, bluntly rounded posteriorly; greatest depth of caudal musculature about one-half depth of caudal fin; musculature extends nearly to tip of tail.

Mouth large; lips having deep lateral folds; two complete rows of papillae on lips; five to seven rows of papillae laterally; beaks moderately developed,

bearing short peglike serrations; moderately wide lateral projections on upper beak; tooth-rows 4/6; upper rows subequal in length; fourth row interrupted medially; length of lower rows 1-4 equal to upper rows; fifth and sixth lower rows shorter; first lower row interrupted medially.

Body brown above; tip of snout brown; venter creamy gray; caudal musculature creamy tan; caudal fin transparent; cream-colored crescent-shaped mark on posterior edge of body; dark brown flecks on caudal musculature and all except anterior two-thirds of ventral caudal fin; large brown square blotches on dorsum of caudal fin; eye reddish brown in life.

Variation.—The variation in size and proportions is given in Table 2. With the exception of one specimen having a short, broken, seventh tooth-row, all specimens have 4/6 tooth-rows that are like those described above. In some specimens the brown blotches on the dorsum of the caudal musculature are fused and marked with cream-colored flecks.

Comparisons.—*Ptychohyla leonhardschultzei* differs from all other members of the *Ptychohyla euthysanota* group in having a square snout, and further differs from *P. spinipollex* in more numerous and smaller nuptial spines and in transverse, instead of posteromedially slanting, vomerine processes between the inner nares. *Ptychohyla leonhardschultzei* differs from *P. euthysanota* in having a rostral keel and in having white flanks boldly spotted with black.

All small hylids that are sympatric with *Ptychohyla leonhardschultzei* are either yellow (*Hyla dendroscarta* and *H. melanomma*) or green (*Hyla erythromma,* which has a red eye, *Hyla hazelae,* which has a black line on the canthus, and *Ptychohyla ignicolor,* which has red flash colors on the thighs).

Life History.—This frog has been found along streams in cloud forests and in pine-oak forest. Males call from vegetation along the stream or from rocks in and at the edge of the stream. The call is a single, long, soft "wraack," repeated at intervals of anywhere from several seconds to three or four minutes. Each note has a duration of 0.62 to 0.95 of a second and a rate of 76 to 78 pulses per second; the dominant frequency falls between 2700 and 2800 cycles per second (Pl. 1C).

Tadpoles were found in several streams in northern Oaxaca. A tadpole having a total length of 21.1 mm. has three upper and four lower tooth-rows well developed; the fourth upper and fifth lower rows are weakly present, and the sixth lower row has not started to develop. Two metamorphosed young have snout-vent lengths of 15.2 and 15.5 mm.

Remarks.—Four specific names have been applied to this species. Ahl (1934:185) based his description of *Hyla leonhardschultzei* on a small, poorly preserved female. Taylor (1944:41) proposed the generic name *Ptychohyla* for a species (named therein as *P. adipoventris*) of hylid having ventrolateral glands and horn-covered nuptial spines. Obviously, Taylor was unaware that *Hyla leonhardschultzei* was the same species. Earlier Taylor (1937:46) described

Hyla pinorum. The types of all of these species came from the Pacific slopes of the Sierra del Sur in Guerrero. Examination of the types and other available specimens shows that they are representatives of a single species. The type of *Hyla pinorum* is an immature male having a snout-vent length of 26.7 mm. All of these specimens have the square snout and black and white flanks characteristic of *Ptychohyla leonhard-schultzei*. Although Shannon (1951:473) based his description of *Hyla milleri* on a male having well-developed ventrolateral glands, he overlooked the presence of these glands in his description and discussion of relationships. The acquisition of more specimens from northern Oaxaca has shown that *Hyla milleri* is the same as *Ptychohyla leonhardschultzei*.

Distribution.—This species is known from pine-oak forest and cloud forest on the Pacific slopes of the Sierra Madre del Sur in Guerrero and Oaxaca and from the Atlantic slopes of the Sierra Madre Oriental in northern Oaxaca. Specimens have been collected at elevations between 700 and 1650 meters. Probably the species occurs in humid forests at similar elevations around the eastern end of the Mexican Highlands in Oaxaca.

Specimens examined.—MEXICO: *Guerrero:* Agua del Obispo, CNHM 123489-90, 126651, 106300, MCZ 29639, UIMNH 25047, 25049, USNM 114551; Malinaltepec, ZMB 34351, 34353. *Oaxaca:* 2.5 km. N of La Soledad, KU 58061; San Lucas Camotlán, UIMNH 3201, USNM 123700-1; Vista Hermosa, KU 64116-7, 64119, 68560 (tadpoles), 71344, 71717-8 (tadpoles), UMMZ 119604; 5 km. S of Yetla, KU 60045 (tadpoles); 7.5 km. S of Yetla, KU 64118, 68556-7 (tadpoles), 68559 (tadpoles), 68561 (2 young), 68630 (skeleton), UMMZ 115514-5, 118863 (tadpoles); 9 km. S of Yetla, KU 68558 (tadpoles).

Ptychohyla spinipollex (Schmidt)

Hyla euthysanota, Dunn and Emlen, Proc. Acad. Nat. Sci. Philadelphia, 84:25, March 22, 1932.

Hyla spinipollex Schmidt, Proc. Biol. Soc. Washington, 49:45-46, May 1, 1936 [Holotype.—MCZ 21300 from the mountains behind Ceiba, Depto. Atlantidad, Honduras; Raymond E. Stadelman collector]. Stuart, Misc. Publ. Mus. Zool. Univ. Michigan, 69:32-34, figs. 5-6, June 12, 1948; Contr. Lab. Vert. Biol. Univ. Michigan, 45:22, 52, 54, 57, May, 1950; Proc. Biol. Soc. Washington, 67:169, August 5, 1954.

Ptychohyla spinipollex, Stuart, Contr. Lab. Vert. Biol. Univ. Michigan, 68: 48, November, 1954. Duellman, Univ. Kansas Publ. Mus. Nat. Hist., 13:351, April 27, 1961.

Diagnosis.—Rostral keel present; snout in lateral profile rounded above; eyelid nearly as wide as interorbital region; flanks white with brown spots; belly spotted; nuptial spines pointed and moderate in size.

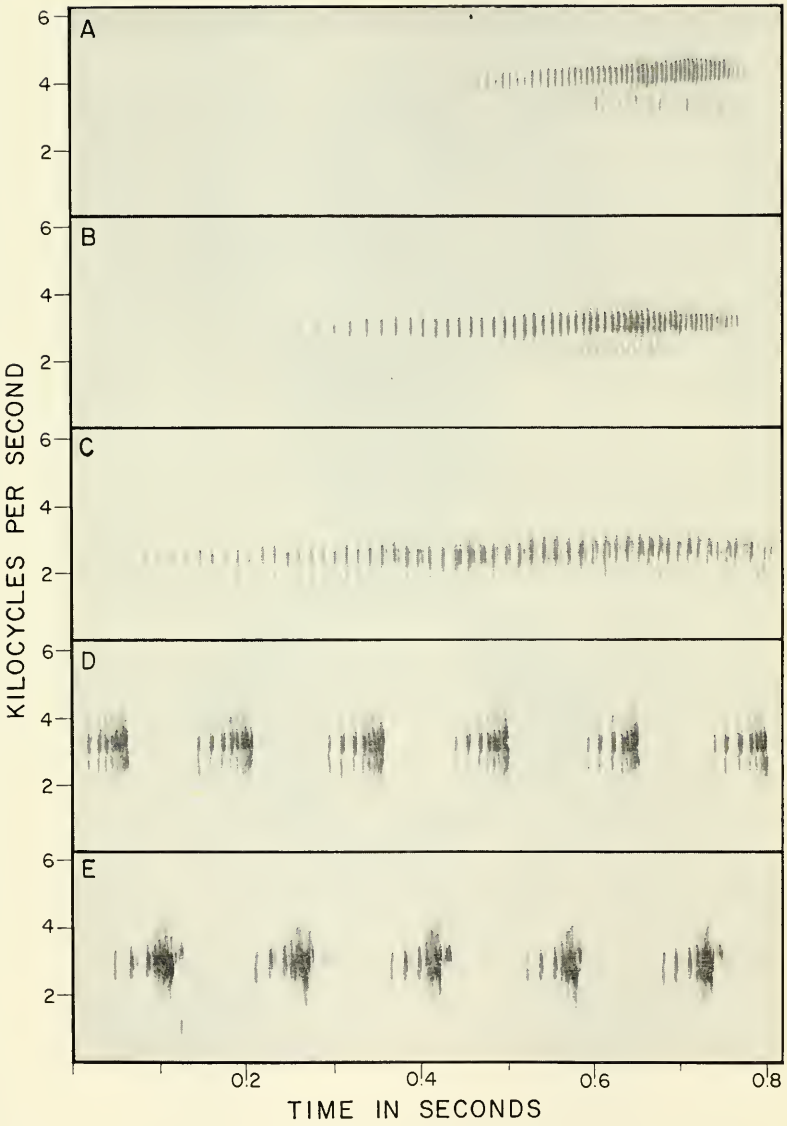
Description.—The following description is based on KU 58054 from Finca Los Alpes, Depto. Alta Verapaz, Guatemala (Pl. 5). Adult male having a snout-vent length of 37.7 mm.; tibia length, 18.2 mm.; tibia length/snout-vent length, 48.2 per cent; foot length, 15.8 mm.; head length, 11.7 mm.; head length/snout-vent length, 31.0 per cent; head width, 11.7 mm.; head width/snout-vent length, 31.0 per cent; diameter of eye, 3.6 mm.; diameter of tympanum, 1.9 mm.; tympanum/eye, 52.7 per cent. Snout in lateral profile

nearly square, slightly rounded above, and in dorsal profile rounded with a pointed tip resulting from vertical rostral keel; canthus pronounced; loreal region barely concave; lips thick, rounded, and barely flaring; nostrils protuberant; internarial distance, 3.0 mm.; top of head flat; interorbital distance, 3.7 mm., about equal to width of eyelid, 3.6 mm. A heavy dermal fold from posterior corner of eye above tympanum to point above insertion of forearm, covering upper edge of tympanum; tympanum round, its diameter equal to its distance from eye. Forearm moderately robust, having faint dermal fold on wrist; row of low, rounded tubercles along ventrolateral edge of forearm; pollex only slightly enlarged, bearing triangular patch of moderate-sized, pointed, horn-covered spines (38 on right, 43 on left); second finger noticeably shorter than fourth; subarticular tubercles round, distal one on fourth finger bifid; discs of fingers of moderate size, that of third finger slightly smaller than diameter of tympanum; vestigial web between first and second fingers; other fingers one-third webbed. Heels broadly overlapping when hind limbs adpressed; tibiotarsal articulation reaches to middle of eye; distinct, but low, tarsal fold extending length of tarsus; inner metatarsal tubercle elevated, flat, and elliptical; outer metatarsal tubercle small and round, near base of fourth toe; row of low indistinct tubercles from heel to base of fifth toe; subarticular tubercles round; length of toes from shortest to longest 1-2-3-5-4, the third and fifth being about equal in length; third and fifth toes webbed to base of disc; fourth toe webbed to base of penultimate phalanx; discs of toes slightly smaller than those on fingers. Anal opening near upper edge of thighs; opening bordered laterally by moderately heavy dermal folds and ventrolaterally by tubercles. Skin of dorsum and ventral surfaces of forelimbs and shanks smooth; that of throat, belly, and ventral surfaces of thighs granular. Ventrolateral glands barely evident. Tongue ovoid, barely notched behind and slightly free posteriorly; vomerine teeth 2-3, situated on \ /-shaped elevations between round inner nares; openings to vocal sac large, one situated along inner posterior edge of each mandibular ramus.

Dorsal ground-color of head, body, and limbs grayish tan with dark brown reticulations on head and body and dark brown transverse bars or spots on limbs; first and second fingers cream color; third and fourth fingers and webbing on hands pale grayish brown; anterior surfaces of thighs reddish tan; posterior surfaces of thighs yellowish tan; tarsi and toes pale grayish tan with brown flecks; webbing on foot pale brown; faint white stripe along ventrolateral edges of tarsi and forearms; narrow white line above and beside anal opening; no white stripe on edge of upper lip; axilla pale flesh-color; throat, chest, and ventral surfaces of limbs pale creamy gray; belly white with scattered brown flecks; flanks grayish white with dark brown flecks; ventral surfaces of tarsi dark brown; ventrolateral glands grayish tan.

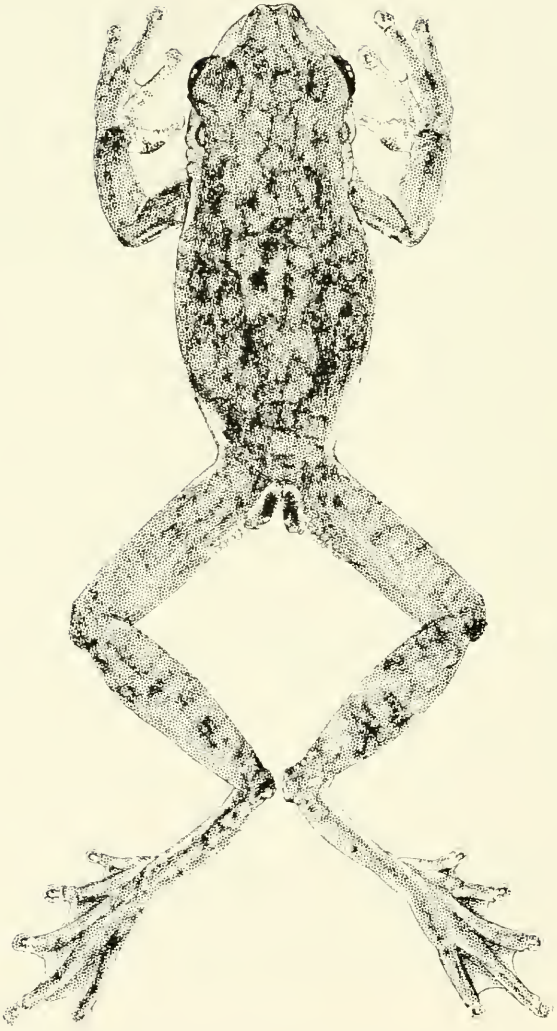
In life the dorsal ground-color of the head, body, fore limbs, and thighs was yellowish tan (Pinkish Buff); dorsal surfaces of shanks and tarsi pale yellowish tan (Pale Pinkish Buff); markings on head and back brown (Snuff Brown) to dark brown (Chocolate); dark bands on limbs brown (Tawny-Olive); first and second fingers creamy tan (Light Pinkish Cinnamon); posterior surfaces of thighs creamy tan (Light Pinkish Cinnamon); third and fourth fingers and webbing on hand grayish brown (Avellaneous); webbing on feet dark brown (Olive Brown); axilla pale pink (Hydrangea Pink); flanks buff

PLATE 11



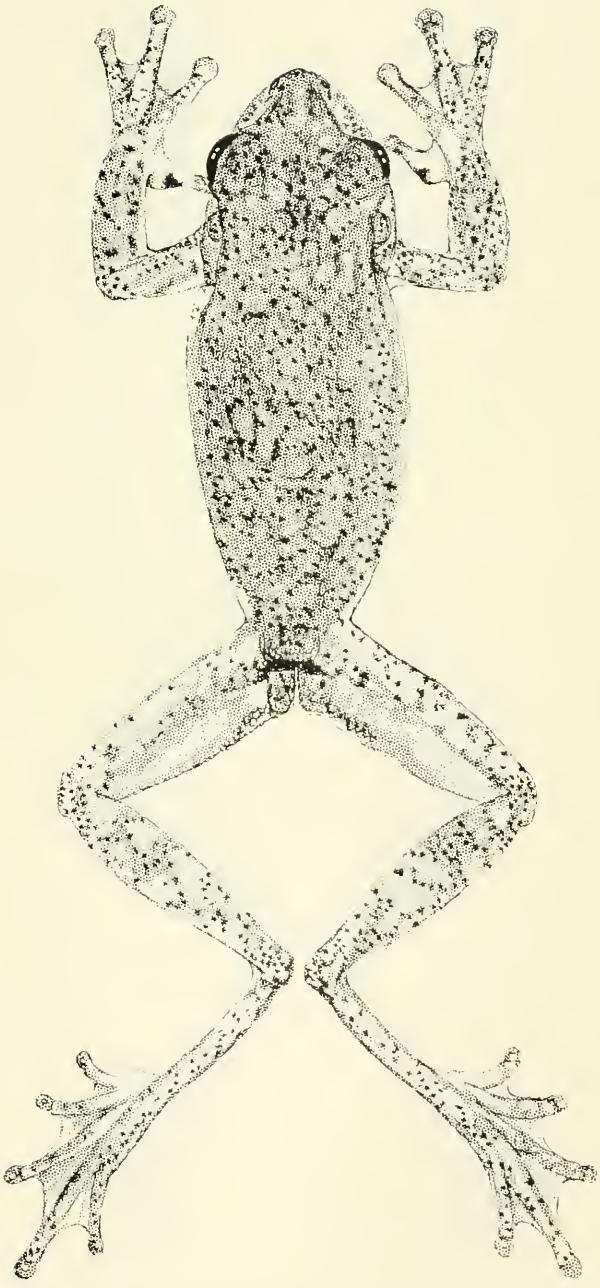
Audiospectrographs of the breeding calls of the five species of *Ptychohyla:* (A) *P. spinipollex* (KU Tape No. 41), (B) *P. euthysanota macrotympanum* (KU Tape No. 48), (C) *P. leonhardschultzei* (UMMZ Tape No. 525), (D) *P. schmidtorum chamulae* (KU Tape No. 52), (E) *P. igunicolor* (UMMZ Tape No. 526).

PLATE 12



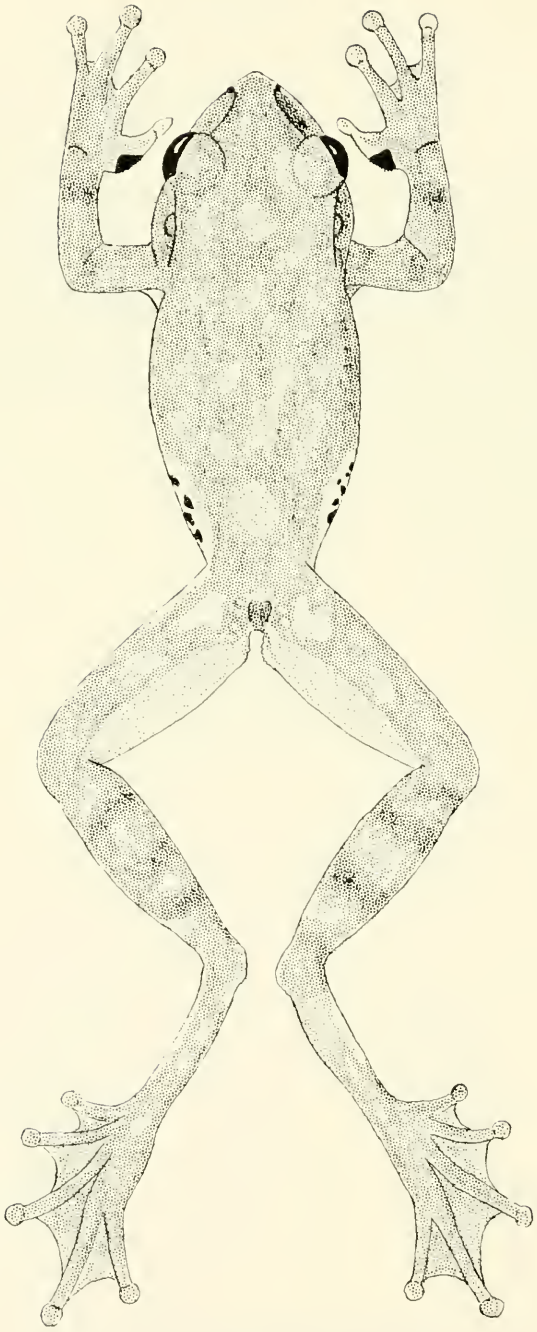
Ptychohyla euthysanota euthysanota (KU 58008).
× 2.

PLATE 13



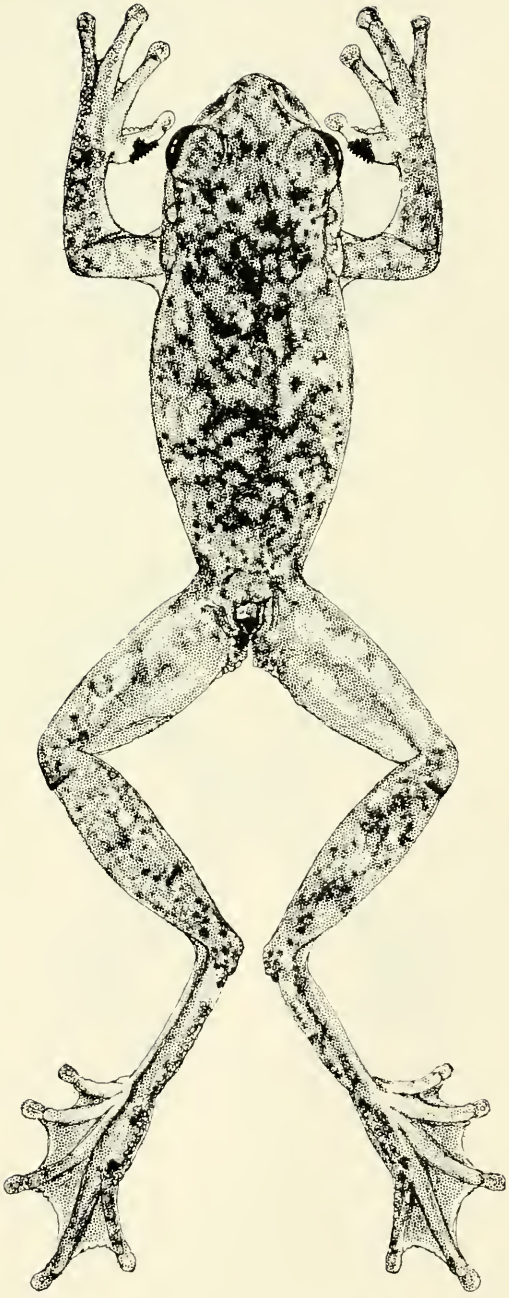
Ptychohyla euthysanota macrotympanum (KU 58049). × 2.

PLATE 14



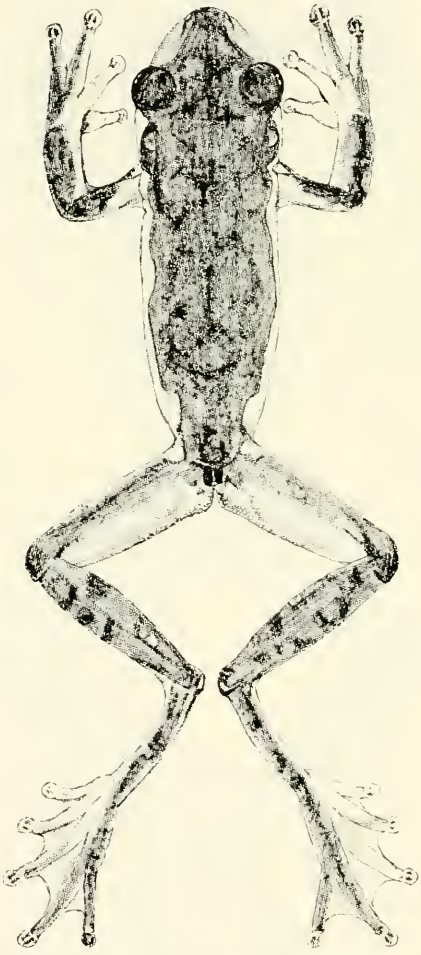
Ptychohyla leonhardschultzei (KU 64117). × 2.

PLATE 15



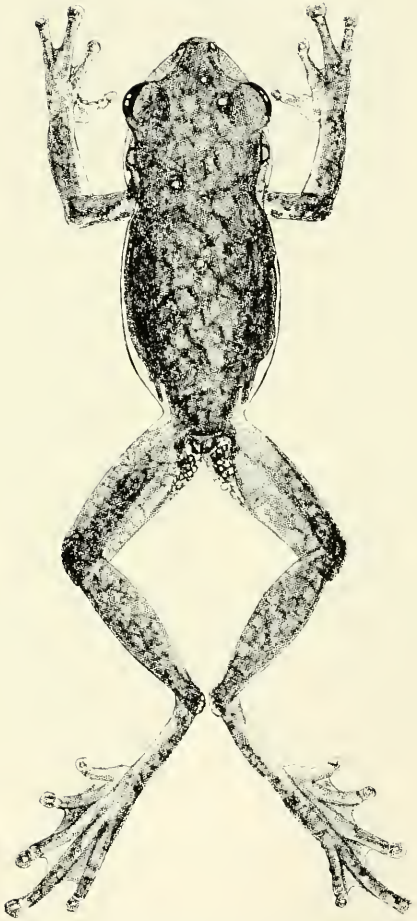
Ptycholyla spinipollex (KU 58054). × 2.

PLATE 16



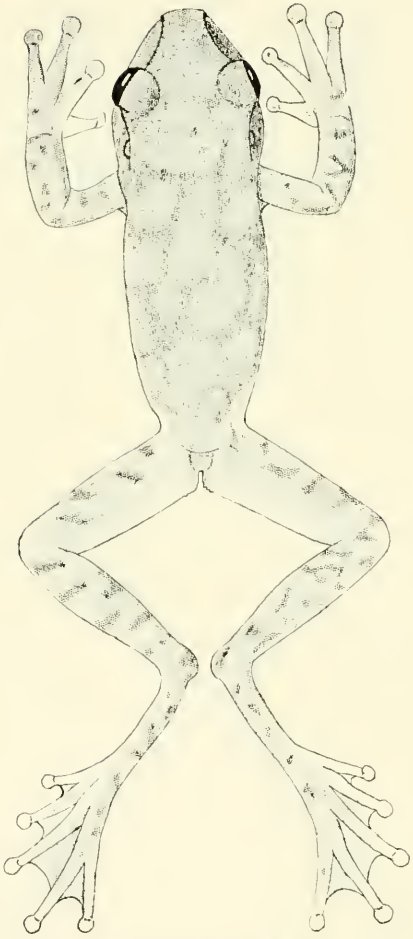
Ptychohyla schmidtorum schmidtorum (KU 58043). × 2.

PLATE 17



Ptychohyla schmidtorum chamulae (KU 58069). × 2.

PLATE 18



Ptycholyla ignicolor (UMMZ 119603).
× 2.

(Cream-Buff) becoming yellow (Lemon Chrome) in groin; spots on flanks dark brown (Clove Brown); iris dull grayish bronze (Orange-Citrine).

Variation.—The distal subarticular tubercle beneath the fourth finger is bifid in about two-thirds of the specimens; in the rest it is round. The posterior edge of the tongue varies from being emarginate to shallowly notched. In most specimens the row of tubercles along the outer edge of the tarsus is made up of discrete tubercles, but in some individuals the tubercles form a nearly continuous dermal fold. Most specimens have the vomerine teeth situated on \ /-shaped elevations, but in some individuals the elevations are more nearly transversely situated between the inner nares.

All 42 specimens from Finca Los Alpes, Guatemala, have dark brown spots and flecks on the venter. Some individuals have only a few flecks on the throat and a few large spots on the flanks, as does KU 64125. Other specimens, such as KU 64132, have dense spotting over the entire venter. The color of the dorsum varies from pale tan to dark brown with darker brown markings; the white line above the anus is present in all specimens, but in some it is indistinct. KU 58053 and 64127 have a dark brown dorsum with large pale tan, square blotches; in life the blotches were pale tan (Pinkish Buff); the rest of the dorsum was dark brown (Sayal Brown). KU 58052 is dark brown with many small white flecks on the dorsum; in life the dorsum was deep olive brown (Dark Olive).

Aside from the differences mentioned above, all specimens from Guatemala are similar in coloration. Three specimens from Honduras (MCZ 21300 and UMMZ 113102-3) have unspotted white venters. MCZ 21300, the holotype of *P. spinipollex,* lacks a white stripe above the anal opening, whereas the stripe is indistinct in UMMZ 113102-3.

Description of tadpole.—The following description is based on KU 60053 from Fina Los Alpes, Depto. Alta Verapaz, Guatemala (Figs. 4D and 6D). No limb buds; total length, 37.2 mm.; body length, 12.2 mm.; body length/total length, 32.8 per cent. Body rounded, not depressed, as wide as deep, ovoid in dorsal profile; mouth directed ventrally; eyes small, directed dorsolaterally; nostrils barely protuberant and directed anterolaterally, somewhat closer to eye than snout; spiracle sinistral and posteroventrad to eye; anal tube dextral. Caudal fin low, bluntly rounded posteriorly; greatest depth of caudal musculature about one-half depth of caudal fin; musculature extends nearly to tip of tail.

Mouth large; lips having deep lateral folds; two complete rows of papillae on lips; six or seven rows of papillae laterally; beaks moderately developed, bearing fine blunt serrations; slender lateral projections on upper beak; tooth-rows 4/7; upper rows subequal in length; fourth row interrupted medially; lower rows 1-4 equal in length to upper rows; lower rows 5-7 decreasing in length; first lower row interrupted medially.

Top of head and tip of snout brown; venter creamy gray; caudal musculature tan; caudal fin transparent; faint cream-colored, narrow, crescent-shaped mark on posterior edge of body, not bordered posteriorly by dark brown mark; brown flecks scattered on caudal musculature and caudal fin; only a few flecks on anterior half of ventral caudal fin; eye bronze-color in life.

Variation.—The variation in size and proportions as compared with tadpoles of other species is given in Table 2. Of the 57 tadpoles of this species that I

have examined, 21 have only six lower tooth-rows, although in some of these specimens a faint ridge for a seventh row is present. In those specimens having seven lower rows, the seventh often is broken.

There is considerable variation in coloration. None has a distinct cream-colored, crescent-shaped mark bordered posteriorly by a dark brown bar or triangle, as in the other species in the *Ptychohyla euthysanota* group. Most specimens have a rather indistinct crescent; some have no crescent. In a few specimens there is a weakly outlined dark mark posterior to the crescent. Some specimens in a series of tadpoles from 32 kilometers north of Morazán, Baja Verapaz, Guatemala, have faint dorsal blotches on the dorsal musculature, much like those in tadpoles of *Ptychohyla leonhardschultzei.*

Comparisons.—*Ptychohyla spinipollex* differs from all other species in the genus by having moderate-sized, instead of small, pointed nuptial spines; also it has fewer spines than the other species (see discussion of this character in Analysis of Data). The nearly equal interorbital breadth and width of the upper eyelid also is diagnostic of this species.

Other hylids sympatric with *Ptychohyla spinipollex* include three species of *Plectrohyla,* each of which has a bony prepollex, heavy body, and rugose skin on the dorsum. The only other sympatric hylid that could be confused with *Ptychohyla spinipollex* is *Hyla bromeliacea,* which has a round snout and yellowish tan dorsum not marked with dark brown.

Life History.—At Finca Los Alpes, Guatemala, in July, 1960, and in August, 1961, calling males were found on bushes and trees along cascading mountain streams. The breeding call consists of a soft "wraack," repeated at intervals of 45 seconds to four minutes. Each note has a duration of about .46 of a second and a rate of 147 pulses per second. The dominant frequency is 4300 cycles per second (Pl. 1A).

Tadpoles have been found in cascading mountain streams. Two metamorphosed young have snout-vent lengths of 15.0 and 15.5 mm.

Remarks.—There is little doubt that all of the specimens herein referred to *Ptychohyla spinipollex* are conspecific. However, the three specimens from Honduras, including the type of *Ptychohyla spinipollex,* differ from Guatemalan specimens in lacking all dark spotting on the venter. Additional specimens from Honduras and eastern Guatemala may show that two subspecies are recognizable, in which case the nominal subspecies will be the population in Honduras.

Distribution.—This species lives in cloud forests at elevations of 800 to 1700 meters on the Atlantic side of the Guatemalan Highlands from the Sierra de Cuchumatanes in western Guatemala eastward to central Honduras.

Specimens examined.—Guatemala: *Alta Verapaz:* Finca Chichén, UMMZ 90876 (tadpoles); Finca Los Alpes, KU 58052-60, 59939 (skeleton), 60053 (tadpoles), 64122-41, 68562, 68563 (tadpoles), 68631-2 (skeletons), MCZ 35000-1, UMMZ 90873, 90874 (3), 90875 (tadpoles); La Primavera, UMMZ 90877 (tadpoles); Panzamalá, UMMZ 90878 (tadpoles). *Baja Verapaz:* 32

km. N of Morazán, KU 68564 (tadpoles); *Santa Elena,* UMMZ 98119, 98120 (2). *Huehuetenango:* 1 km. E of Barillas, UMMZ 123136-7 (tadpoles). *Progreso:* Finca Bucaral, UMMZ 106783 (3), 123138 (tadpoles), S-1292 (skelton).

HONDURAS: *Atlantidad:* Mountains behind Ceiba, MCZ 21300. *Morazán:* Cerro Uyuca, UMMZ 123102-3.

The *Ptychohyla schmidtorum* Group

Two species in group; adults having only vestige of web between fingers and lacking tarsal fold; pollex of breeding males lacking spinous, horny, nuptial tuberosities; mouth of tadpole greatly expanded, funnel-shaped, lacking lateral folds, and having ⅗ tooth-rows; breeding call consisting of series of short notes.

Ptychohyla schmidtorum

Diagnosis.—Diameter of tympanum more than half of diameter of eye; internarial region depressed; toes three-fourths webbed; no red flash-colors on thighs.

Ptychohyla schmidtorum schmidtorum Stuart

Ptychohyla schmidtorum Stuart, Proc. Biol. Soc. Washington, 67:169-172, August 5, 1954 [Holotype.—CNHM 27055 from El Porvenir (17 kilometers air-line west of San Marcos), Depto. San Marcos, Guatemala; Karl P. Schmidt collector]. Duellman, Univ. Kansas Publ. Mus. Nat. Hist., 13:351, 355, April 27, 1961.

Diagnosis.—Vomerine teeth 5-11; dorsum dark brown; white spot below eye; eye red in life.

Description.—The following description is based on KU 58043 from Finca La Paz, Depto. San Marcos, Guatemala (Pl. 6). Adult male having snout-vent length of 31.6 mm.; tibia length, 15.0 mm.; tibia length/snout-vent length, 47.5 per cent; foot length, 12.5 mm.; head length, 10.2 mm.; head length/snout-vent length, 32.3 per cent; head width, 9.9 mm.; head width/snout-vent length, 31.3 per cent; diameter of eye, 3.4 mm.; diameter of tympanum, 1.8 mm.; tympanum/eye, 52.9 per cent. Snout in lateral profile nearly square, slightly rounded above and below, and in dorsal profile bluntly squared; canthus pronounced; loreal region concave; lips thick, rounded, and flaring; nostrils protuberant; internarial distance, 2.2 mm.; internarial region depressed; top of head flat; interorbital distance, 3.4 mm., much greater than width of eyelid, 2.5 mm. Thin dermal fold from posterior corner of eye above tympanum to insertion of forelimb, covering upper edge of tympanum; tympanum round, its diameter equal to its distance from eye. Forearm slender, lacking distinct dermal fold on wrist; row of low rounded tubercles along ventrolateral edge of forearm; pollex slightly enlarged; no nuptial spines; second and fourth fingers about equal in length; subarticular tubercles small and round, distal one beneath fourth finger bifid; discs small, that of third finger noticeably smaller than tympanum; no web between first and second fingers; vestige of web between other fingers. Heels overlap when hind limbs adpressed; tibiotarsal articulation reaches to middle of eye; no tarsal fold; inner metatarsal tubercle large, flat, and elliptical; outer metatarsal tubercle small, ovoid, slightly more distal than inner; subarticular tubercles round; length of digits from shortest to longest 1-2-5-3-4; third and fifth toes webbed to base of discs; fourth toe webbed to base of penultimate phalanx; discs of toes smaller

than on fingers. Anal opening directed posteriorly at upper edge of thighs; no anal flap; pair of large tubercles below anal opening and smaller tubercles farther below. Skin of dorsum and ventral surfaces of forelimbs and shanks smooth; that of belly and ventral surfaces of thighs granular. Ventrolateral glands well developed, reaching axilla and groin and narrowly separated on chest. Tongue ovoid, emarginate posteriorly, and only slightly free behind; vomerine teeth 3-3, situated on small triangular elevations between ovid inner nares; openings to vocal sac large, one situated along inner posterior edge of each mandibular ramus.

Dorsum of head, body, and limbs reddish brown with indistinct, irregular darker brown markings on body and dark brown transverse bands or spots on limbs; first and second fingers creamy white; third and fourth fingers brown; dorsal surfaces of tarsi and third, fourth, and fifth toes tan with brown spots; first and second toes and webbing on feet creamy tan; enamel-white stripe along edge of upper lip continuing over, and on posterior edge of, forearm to groin, expanded to form spot below eye; belly white, unspotted; ventrolateral glands pale brown; ventral surfaces of hind limbs and anterior and posterior surfaces of thighs cream color; enamel-white stripe on heel; creamy white stripe along ventrolateral edges of tarsi and forearms.

In life dorsum reddish brown (Terra Cotta) with dark brown (Burnt Umber) markings; first and second fingers and first and second toes orange-yellow (Light Orange-Yellow); posterior surfaces of thighs pale reddish tan (Ochraceous-Salmon); webbing on feet yellowish tan (Deep Colonial Buff); belly white; iris red (Nopal Red).

Variation.—Little variation in structural characters was observed. All but five specimens have bifid subarticular tubercles beneath the fourth finger. Three specimens have cordiform tongues, and in four others the tongue is ovoid and shallowly notched behind; all other specimens have an emarginate ovoid tongue.

Some individuals when active at night had a pale brown (Ochraceous-Tawny) dorsum with dull olive green (Dark Olive Buff) markings. Otherwise there was no noticeable variation in color.

Description of tadpole.—The following description is based on KU 60051 from Finca La Paz, Depto. San Marcos, Guatemala (Figs. 5A and 6E). Small hind limbs; total length, 37.9 mm.; body length, 11.6 mm.; body length/total length, 30.6 per cent. Body only slightly depressed, nearly as deep as wide, in dorsal profile ovoid, widest just posterior to eyes; in lateral profile snout rounded; mouth directed ventrally; eyes small, directed dorsolaterally; nostrils barely protuberant, directed anteriorly, somewhat closer to eye than snout; spiracle sinistral and posteroventrad to eye; anal tube dextral. Tail long and slender; caudal fin low and rounded posteriorly; depth of caudal musculature one-half greatest depth of caudal fin; musculature not extending to tip of tail.

Mouth large; thin fleshy lips greatly expanded and forming large funnel-shaped disc; width of mouth two-thirds greatest width of body; outer edge of lips having one row of small papillae; inner surfaces of mouth smooth; scattered large papillae forming one nearly complete row around teeth; other large papillae laterally; beaks moderately developed, bearing long, pointed denticulations; no lateral projections on upper beak; tooth-rows $\frac{2}{3}$, all short; second and third upper rows subequal in length; first upper row shorter; first

and third upper rows interrupted medially; first lower row interrupted medially, equal in length to second and third upper rows; second lower row slightly shorter; third lower row shortest.

Body mottled brown and creamy gray above and below; mouth colored like body; caudal musculature creamy tan; caudal fin transparent; dark brown streak mid-laterally on anterior third of caudal musculature; rest of tail and all of caudal fin heavily flecked with brown; eye red in life.

Variation.—The third upper tooth-row is interrupted in all specimens; in some individuals the first upper and first lower rows are complete. The variation in size and proportions is given in Table 2. The dark brown lateral streak on the anterior part of the caudal musculature is distinct on most specimens; the only other variation in coloration is in the amount of brown flecking on the caudal musculature and fin.

Comparisons.—*Ptychohyla schmidtorum schmidtorum* differs from *P. schmidtorum chamulae* as stated in the diagnosis and in having pale creamy tan, as opposed to dark brown, webbing on the feet; and from *P. ignicolor* in having a depressed, as opposed to a flat, internarial region. Tadpoles of *P. s. schmidtorum* have a mottled appearance, as opposed to the more uniform brown color of *P. s. chamulae.*

Ptychohyla schmidtorum schmidtorum and several species of *Plectrohyla* are sympatric. All species of the latter genus have a bony prepollex, rugose skin on the dorsum, and heavy body; also sympatric is *Ptychohyla e. euthysanota,* which has a tarsal fold and in breeding males spinous nuptial tuberosities.

Life History.—This species breeds in clear mountain streams where males call from vegetation along the stream. The call consists of series of short notes, three to nine notes per series, sounding like "raa-raa-raa." The duration of each note is approximately .065 of a second, and has a rate of 96 to 119 pulses per second; the dominant frequency is about 3400 cycles per second. The call is almost indistinguishable from that of *Ptychohyla schmidtorum chamulae.*

Tadpoles and metamorphosing young were found at Finca La Paz, Guatemala, in late July, 1960. Two young lacking tails but not having completely developed mouths have snout-vent lengths of 14.2 and 14.6 mm. L. C. Stuart collected four metamorphosing young at Finca La Paz on May 6, 1949. By May 10 the frogs were completely metamorphosed, at which time they had snout-vent lengths of 15.5 to 17.0 (average 16.1) mm.

Remarks.—There is no doubt that this frog is most closely related to *Ptychohyla schmidtorum chamulae,* even though the ranges of the two subspecies are separated by the interior depression of Chiapas. Since at least at Finca La Paz, Guatemala, *P. s. schmidtorum* occurs with *P. e. euthysanota,* it is surprising that the former species has not been found at more localities along the Pacific slopes

on northern Central America. At Finca La Paz in July, 1960, *P. s. schmidtorum* was more abundant than *P. e. euthysanota.*

Distribution.—This species is known only from a limited area at elevations between 1300 and 2200 meters on the Pacific slopes of the Sierra Madre in extreme eastern Chiapas and western Guatemala.

Specimens examined.—Mexico: *Chiapas:* Finca Irlandia, UMMZ 105429-30. Guatemala: *San Marcos:* El Porvenir, CNHM 20755, 20761, 69904, UMMZ 80918; Finca La Paz, 2 km. W of La Reforma, KU 58016-44, 59940-2 (skeletons), 60050 (3 young), 60051 (tadpoles), 60052 (4 young), MCZ 34998-9, UMMZ 123144-7 (tadpoles).

Ptychohyla schmidtorum chamulae Duellman

Ptychohyla chamulae Duellman, Univ. Kansas Publ. Mus. Nat. Hist., 13: 354-357, pl. 25, fig. 2, April 27, 1961 [Holotype.—KU 58063 from 6.2 kilometers south of Rayón Mescalapa, Chiapas, México; William E. Duellman collector].

Diagnosis.—Vomerine teeth 4-6; dorsum bright green; white lateral stripe; eye reddish bronze in life.

Description.—The following description is based on KU 58069 from 6.2 kilometers south of Rayón Mescalapa, Chiapas, México (Pl. 7). Adult male having a snout-vent length of 27.6 mm.; tibia length, 13.0 mm.; tibia length/snout-vent length, 47.1 per cent; foot length, 10.8 mm.; head length, 9.6 mm.; head length/snout-vent length, 34.7 per cent; head width, 9.2 mm.; head width/snout-vent length, 33.1 per cent; diameter of eye, 3.0 mm.; diameter of tympanum, 1.6 mm.; tympanum/eye, 53.3 per cent. Snout in lateral profile nearly square, slightly rounded above and below, and in dorsal profile blunt, almost square; canthus pronounced; loreal region concave; lips thick, rounded and flaring; nostrils protuberant; internarial distance, 2.5 mm.; internarial region slightly depressed; top of head flat; interorbital distance, 3.3 mm., much greater than width of eyelid, 2.5 mm. Thin dermal fold, from posterior corner of eye above tympanum to insertion of fore limb, covering upper edge of tympanum; tympanum nearly round, its diameter equal to its distance from eye. Forearm slender, lacking distinct fold on wrist; row of low, rounded tubercles on ventrolateral surface of forearm; pollex slightly enlarged, without nuptial spines; second and fourth fingers equal in length; subarticular tubercles round, that under fourth finger bifid; discs small, that of third finger noticeably smaller than tympanum; no web between first and second fingers; vestige of web between other fingers. Heels overlapping when hind limbs adpressed; tibiotarsal articulation reaches to middle of eye; no tarsal fold; inner metatarsal tubercle large, flat, and elliptical; outer metatarsal tubercle small, elliptical, slightly more distal than inner; subarticular tubercles round; length of digits from shortest to longest 1-2-5-3-4; third and fifth toes webbed to base of disc; fourth toe webbed to base of penultimate phalanx; discs smaller on toes than on fingers. Anal opening directed posteriorly at upper edge of thighs; no anal flap; pair of large tubercles below anal opening. Skin of dorsum and of ventral surfaces of forelimbs and shanks smooth; that of throat, belly, and ventral surfaces of thighs granular. Ventrolateral glands well developed, not reaching axilla or groin and broadly separated midventrally. Tongue cordiform, shallowly notched behind and only slightly free posteriorly; vomerine teeth 2-3, situated on small triangular elevations be-

tween ovoid inner nares; openings to vocal sac large, one situated along inner posterior edge of each mandibular ramus.

Dorsum of head, body and limbs reddish brown with dark purplish brown markings on back and shanks; first finger creamy tan; other fingers pale brown; dorsal surfaces of tarsi, third, fourth, and fifth toes dull tan with brown spots; first and second toes creamy tan; webbing on feet brown; anterior and posterior surfaces of thighs tan; faint creamy white stripe along ventrolateral edges of tarsi and forearms; enamel-white stripe on heel; axilla and groin gray; enamel-white stripe on edge of upper lip, continuing onto proximal upper surfaces of forelimb and on flanks to groin, widened under eye to form large spot, and bordered below on flanks by dark brown stripe; white stripe above and white spots below anal opening; throat and chest white; belly and ventral surfaces of limbs cream color; brown dash on either side of chin and brown spot on throat near angle of jaws; few brown flecks on belly; ventrolateral glands orange-tan; ventral surfaces of tarsi and feet brown.

In life, dorsal surfaces of head, body, and limbs bright green (Shamrock Green); first and second fingers pale orange (Apricot Yellow); stripe on upper lip and spot below eye enamel-white; stripe on flanks silvery white, bordered below by brown (Saccardo's Umber) brown; anterior and posterior surfaces of thighs yellowish brown (Old Gold); webbing of feet dull brown (Brownish Olive); belly deep yellow (Amber Yellow); iris reddish bronze (English Red).

Variation.—Tubercles beneath the fourth fingers are bifid in 20 specimens and rounded in all others. The tongue is emarginate in 12 specimens and cordiform in all others. In most specimens the white stripe on the upper lip continues onto the flanks and to the groin; in five specimens the stripe terminates above the forearm, and in three it terminates at mid-flank. The lateral stripe is absent in two specimens. All specimens were uniform green above when found at night; later some changed to pale green (Light Oriental Green) on the dorsum with irregular yellowish tan (Naples Yellow) blotches. Most males have brown flecks on the throat and ventrolateral gland, but some specimens are immaculate below, and one has dark brown mottling on the throat. Several males have a round, orange-tan glandular area on the chin, as does *P. ignicolor.*

Description of tadpole.—The following description is based on KU 58199 from 6.2 kilometers south of Rayón Mescalapa, Chiapas, México (Figs. 5B and 6F). Hind limbs small; total length, 39.0 mm.; body length, 10.5 mm.; body length/total length, 26.9 per cent. Body barely depressed, only slightly wider than deep, widest just posterior to eyes; in dorsal profile ovoid; mouth directed ventrally; eyes small, directed dorsolaterally; nostrils barely protuberant, directed anterodorsally, slightly closer to eye than snout; spiracle sinistral and posteroventrad to eye; anal tube dextral. Tail long and slender; caudal fin low, rounded posteriorly; depth of caudal musculature one-half greatest depth of caudal fin; musculature not extending to tip of tail.

Mouth large; thin fleshy lips greatly expanded and forming funnel-shaped disc; outer edge of lips having one row of small papillae; inner surfaces of mouth smooth; scattered large papillae forming nearly one complete row around teeth; other papillae laterally; beaks moderately developed, bearing long, pointed denticulations; no lateral projections on upper beak; tooth-rows ⅔, all short; second and third upper rows subequal in length; first upper row shorter; first and third upper rows interrupted medially; first lower row inter-

rupted medially, equal in length to second and third upper rows; second lower row slightly shorter; third lower row shortest.

Body dark brown above and dark gray below; fleshy part of mouth creamy gray mottled with dark brown; caudal musculature pale tan with heavy suffusion of brown flecks; caudal fin transparent with brown spots; dark brown streak mid-laterally on anterior one-fifth of caudal musculature, bordered below by cream-colored spot; eye brown in life.

Variation.—The third upper tooth-row is interrupted in all specimens, but in some individuals the first upper row and first lower row are complete. The only noted variation in color is the intensity of brown pigmentation on the caudal musculature, which in most specimens is sufficiently dense to make the tail look brown. In some specimens the mid-lateral streak is indistinct, and the pale spot below the streak is absent.

Comparisons.—Aside from the characters listed in the diagnosis, *Ptychohyla schmidtorum chamulae* differs from *P. schmidtorum schmidtorum* by having dark brown webbing on the feet, instead of pale creamy tan webbing, and in having in life a yellow venter, instead of a white venter. *Ptychohyla ignicolor* also is green in life, but has red flash-colors on the thighs, red webbing on the feet, and lacks the white lateral stripe diagnostic of *P. schmidtorum chamulae.*

Plectrohyla matudai matudai and *P. guatemalensis* are sympatric with *Ptychohyla schmidtorum chamulae.* Each of the first two has a bony prepollex, rugose skin on the dorsum, and heavy body. Also living with *Ptychohyla chamulae* are *Hyla chaneque,* a large species having a tuberculate dorsum and webbed fingers, and *Hyla bivocata,* a small yellow species having a broad, flat head, small indistinct tympanum, and an axillary membrane.

Life History.—Calling males were found on leaves of herbs and bushes by cascading streams in cloud forest. The call consists of series of short notes, three to nine notes per series, sounding like "raa-raa-raa." The duration of each note is .054 to .070 of a second, and has a rate of 96 to 110 pulses per second. The dominant frequency falls between 3350 and 3450 cycles per second (Pl. 1D). The call is almost indistinguishable from that of *Ptychohyla schmidtorum schmidtorum.*

Tadpoles were found in the cascading streams; the smallest tadpole has a total length of 17.2 mm. and has only ⅔ tooth-rows. At a stream 6.2 kilometers south of Rayón Mescalapa, Chiapas, metamorphosing young were found on June 16 and August 5, 1960. Each of two completely metamorphosed young has a snout-vent length of 15.7 mm. Another having a snout-vent length of 16.2 mm. has a tail stub 2 mm. long and a completely metamorphosed mouth. Two others have snout-vent lengths of 13.6 and 14.1 mm. and tail lengths of 11.5 and 8.1 mm. respectively; in these the mouth parts are incompletely metamorphosed.

Remarks.—Duellman (1961:354) described *Ptychohyla chamulae*

and stated that it probably was most closely related to *P. schmidtorum*. Further study has revealed additional resemblance in morphological and behavioral details. It is concluded that the two populations are more realistically treated as subspecies than as species. The geographic ranges, as now known, are disjunct. *Ptychohyla schmidtorum chamulae* inhabits cloud forest on the Atlantic slopes of the Chiapan Highlands, whereas *P. s. schmidtorum* lives in cloud forest on the Pacific slopes of the Sierra Madre in Chiapas and Guatemala. Between their known geographic ranges are the pine clad Sierra Madre and Chiapan Highlands, and intervening sub-humid Grijalva Valley.

Distribution.—This species is known only from elevations between 1500 and 1700 meters on the Atlantic slopes of the Chiapan Highlands; it is to be expected in cloud forests on the northern slopes of the Sierra de Cuchumatanes in Guatemala.

Specimens examined.—MEXICO: *Chiapas: 15 km. N of Pueblo Nuevo Solistahuacán,* UMMZ 123325 (4); *16.5 km. N of Pueblo Nuevo Solistahuacán,* UMMZ 123322 (10); *18 km. N of Pueblo Nuevo Solistahuacán,* UMMZ 121395-9, 123324 (8), 123326 (5); *18.6 km. N of Pueblo Nuevo Solistahuacán,* UMMZ 123323 (4); *5.6 km. S of Rayón Mescalapa* KU 58062, 58200 (tadpoles); *6.2 km. S of Rayón Mescalapa,* KU 58063-74, 58199 (tadpole), 58234-8, 59936 (skeleton).

Ptychohyla ignicolor Duellman

Ptychohyla ignicolor Duellman, Uni. Kansas Publ. Mus. Nat. Hist., 13:352-353, pl. 25, fig. 1, April 27, 1961 [Holotype.—UMMZ 119603 from 6 kilometers south of Vista Hermosa, Oaxaca, México; Thomas E. Moore collector].

Diagnosis.—Diameter of tympanum less than one-half diameter of eye; internarial region flat; 3-7 vomerine teeth; toes one-half webbed; no white spot below eye; no lateral white stripe; in life dorsum green; groin and thighs having bright red flash-colors.

Description.—The following description is based on UMMZ 119603 from 6 kilometers south of Vista Hermosa, Oaxaca, México (Pl. 8). Adult male having a snout-vent length of 30.0 mm.; tibia length, 14.6 mm.; tibia length/snout-vent length, 48.7 per cent; foot length, 12.3 mm.; head length, 9.2 mm.; head length/snout-vent length, 30.7 per cent; head width, 9.3 mm.; head width/snout-vent length, 31.0 per cent; diameter of eye, 3.2 mm.; diameter of tympanum, 1.3 mm.; tympanum/eye, 40.6 per cent. Snout in lateral profile square, and in dorsal profile rounded; canthus pronounced; loreal region slightly concave; lips moderately flaring; top of head flat; nostrils protuberant; internarial distance, 2.8 mm.; internarial region flat; interorbital distance, 3.3 mm., much broader than width of eyelid, 2. 8 mm. A heavy dermal fold from posterior corner of eye above tympanum to insertion of forelimb, covering upper edge of tympanum; tympanum elliptical, its greatest diameter equal to its distance from eye. Forearm moderately robust having distinct dermal fold on wrist; pollex moderately enlarged without nuptial spines; second and fourth fingers equal in length; subarticular tubercles round, none is bifid;

discs on fingers moderate in size, that on third finger slightly larger than tympanum; no web between first and second fingers; vestige of web between other fingers. Heels overlap when hind limbs adpressed; tibiotarsal articulation extends to anterior corner of eye; no tarsal fold; inner metatarsal tubercle large, flat, and elliptical; outer metatarsal tubercle near inner one and triangular in shape; subarticular tubercles round; length of digits from shortest to longest 1-2-5-3-4; third toe webbed to proximal end of penultimate phalanx; fourth toe webbed to distal part of antepenultimate phalanx; fifth toe webbed to middle of penultimate phalanx; discs on toes smaller than on fingers. Anal opening directed posteriorly at upper edge of thighs; no anal flap; pair of large tubercles below anal opening; small tubercles ventral and lateral to these. Skin of dorsum and ventral surfaces of limbs smooth; that of throat and belly granular. Ventrolateral glands noticeably thickened, extending from axilla nearly to groin and only narrowly separated midventrally on chest; skin of anterior part of chin thickened and glandular. Tongue cordiform, shallowly notched behind and only slightly free posteriorly; vomerine teeth 0-3, situated on rounded elevations between somewhat larger, round inner nares; openings to vocal sac large, one situated along posterior margin of each mandibular ramus.

Dorsal ground-color of head, body, and limbs dull brown with dark brown reticulations on head and body and dark brown transverse bands or spots on limbs; first and second fingers cream color; third and fourth fingers dull tan; anterior surfaces of thighs pale brown; posterior surfaces of thighs cream color with heavy suffusion of brown; dorsal surfaces of tarsi and third, fourth, and fifth toes dull brown with dark brown spots; first and second toes creamy white; webbing on foot brown; axilla and groin cream color; flanks brown; no white stripes on edge of upper lip or on flank; faint, barely discernible tan streak above anal opening; faint creamy tan line on ventrolateral edges of tarsi; throat, belly, ventral surfaces of limbs, inner edges of tarsi, and first toes cream color; outer ventral surfaces of tarsi and other toes brown; chest and throat spotted with brown; ventrolateral and chin glands orange-brown.

In life the dorsum was uniform green (Cosse Green) becoming paler green (Bright Green-Yellow) on flanks, later changing to paler green (Javel Green) on dorsum with irregular darker green (Lettuce Green) markings and greenish yellow (Green-Yellow) on flanks; anterior and posterior surfaces of thighs, ventral surfaces of shanks, anterior surfaces of tarsi, and upper proximal surfaces of first, second, and third toes red (Coral Red); venter pale creamy yellow (Sulfur Yellow); iris pale golden color (Aniline Yellow).

Variation.—Of 13 specimens, six have a cordiform tongue; the others have an emarginate tongue. Five specimens have round subarticular tubercles beneath the fourth fingers; six specimens have a bifid tubercle on one hand, and two specimens have bifid tubercles on both hands. A round gland is present on the chin of all specimens; in some the gland is barely visible, but in others it is large and distinct. In two specimens the ventrolateral glands are weakly developed; in the others the glands are well developed and orange-tan. The white anal stripe varies from a thin line to a series of white flecks. Dark brown or black flecks are present on the throat, chest, and flanks of all specimens. In some the flecks are small and widely scattered; in others the flecks are larger and more numerous. All specimens were pale green above

when calling at night; later they changed to dull green with darker green reticulations. The flash-colors on the thighs and in the groin vary from red to orange-red or brownish red.

Description of tadpole.—The following description is based on KU 71716 from Vista Hermosa, Oaxaca, México (Figs. 5C and 6G). Hind limbs small; total length, 39.6 mm.; body length, 11.8 mm.; body length/total length, 29.8 per cent. Body moderately depressed, only slightly wider than deep, in dorsal profile ovoid, widest just posterior to eyes; in lateral profile snout rounded; mouth directed ventrally; eyes small, directed dorsolaterally; nostrils barely protuberant, directed anteriorly, somewhat closer to eye than snout; spiracle sinistral and posteroventrad to eye; anal tube dextral. Tail long and slender; caudal fin low and rounded posteriorly; depth of caudal musculature about one-half greatest depth of caudal fin; musculature not extending to tip of tail.

Mouth large; thin fleshy lips greatly expanded and forming large funnel-shaped disc; width of mouth about two-thirds greatest width of body; outer edge of lips having one row of small papillae; inner surface of mouth smooth; scattered large papillae forming one nearly complete row around teeth; other papillae laterally; one large papilla just above each end of first lower tooth-row; beaks moderately developed bearing long, pointed denticulations; no lateral projections on upper beak; tooth-rows $\frac{2}{3}$, all short; second and third upper rows subequal in length; first upper row shorter; first lower row equal in length to second and third upper rows; second lower row slightly shorter; third lower row shortest.

Body creamy gray with dark brown flecks above and below; mouth colored like body; caudal musculature creamy tan; caudal fin transparent; dark brown streak on anterior third of caudal musculature; rest of tail and all of caudal fin, except anterior two-thirds of ventral fin, heavily flecked with brown; iris silvery bronze color in life.

Variation.—The only other known tadpole, which was collected with the individual described above, differs in having only two upper tooth-rows. The first upper tooth-row seems not to have developed.

Comparisons.—From *P. schmidtorum chamulae* and *P. s. schmidtorum, P. ignicolor* differs as follows: Tympanum smaller; snout more nearly square; less webbing on toes; internarial region flat instead of depressed; white lateral stripes lacking.

Ptychohyla ignicolor and several small and moderate sized hylids are sympatric. From *P. ignicolor* these hylids can be distinguished as follows: *Hyla dendroscarta* has a round snout and yellow dorsum; *Hyla erythromma* has a round snout, green dorsum, white flanks, and a red eye; *Hyla hazelae* has a tarsal fold, green dorsum, and a black line on the canthus; and *Ptychohyla leonhardschultzei* has a tarsal fold, brown dorsum, black and white flanks, and horny nuptial spines in breeding males.

Life History.—At Vista Hermosa, Oaxaca, males were calling on vegetation above small streams on March 30, 1959, and on June 28, 1962; males were found on vegetation overhanging a stream 6 kilometers south of Vista Hermosa on June 27 and July 3, 1962. The call consists of a series of short notes, three to thirteen notes per

series, sounding like "raa-raa-raa." The duration of each note is about .08 of a second and has a rate of 123 to 129 pulses per second. The dominant frequency of notes in short series is about 2100 cycles per second, whereas the dominant frequency of notes in long series is about 3150 cycles per second (Pl. 1E).

On June 28, 1962, two tadpoles of this species were found in a quiet pool in a spring-fed rivulet at Vista Hermosa, Oaxaca. Females are unknown.

Remarks.—The absence of a tarsal fold and of nuptial spines in breeding males, the nature of the breeding call, and the form of tadpole are characters that place *Ptychohyla ignicolor* in the *P. schmidtorum*-group.

Distribution.—This species is known from only two localities at elevations of 1500 and 1850 meters in the cloud forest on the northern (Atlantic) slopes of the Sierra Madre Oriental in northern Oaxaca.

Specimens examined.—Mexico: *Oaxaca: Vista Hermosa,* KU 71334, 71716 (tadpoles), UMMZ 119602; 6 km. S of Vista Hermosa, KU 71335-42, 71343 (skeleton), UMMZ 119603, 123327 (2).

DISTRIBUTION AND ECOLOGY

Geographic Distribution of the Species

The distribution of species of *Ptychohyla* reflects the distribution of cloud forest in southern México and northern Central America. The frogs are restricted to mountainous areas, usually at elevations higher than 1000 meters above sea level. *Ptychohyla* does not range to great heights in the mountains, where west of the Isthmus of Tehuantepec the mountain streams are inhabited by frogs of the *Hyla bistincta* group, and in Chiapas and Guatemala by species of *Plectrohyla.*

Frogs of the *Ptychohyla euthysanota* group have a greater combined geographic range than the species comprising the *Ptychohyla schmidtorum* group (Fig. 7). No two species in the same group are sympatric, but members of different groups are sympatric in at least parts of their ranges. Apparently *P. leonhardschultzei* ranges around the southern edge of the Mexican Highlands, where the species occurs on both Atlantic and Pacific slopes; as can be seen from the distribution map, there are many gaps in the known range of this species. The range of *P. euthysanota euthysanota* is along the Pacific slopes of the Sierra Madre in Chiapas, Guatemala, and El Salvador, whereas that of *P. euthysanota macrotympanum* is along the southern interior slopes of the Central Highlands of Chiapas and the Sierra de Cuchumatanes in Guatemala. *Ptychohyla*

spinipollex occurs on the wet Atlantic slopes of the Guatemalan and Honduranean Highlands; the range of the species in Honduras is poorly known.

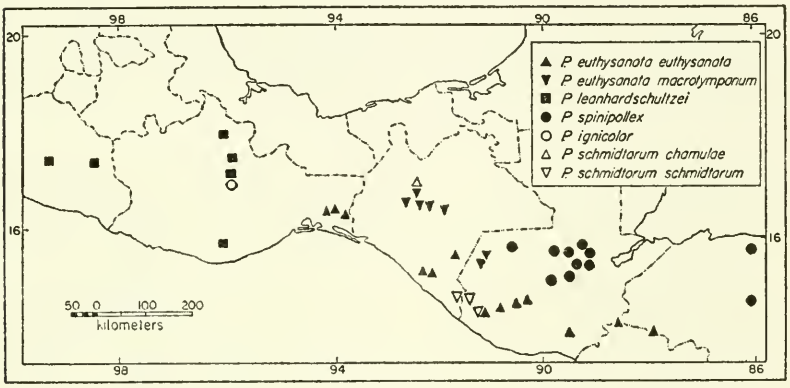


FIG. 7. Map showing locality records for the species and subspecies of *Ptychohyla.*

The frogs of the *Ptychohyla schmidtorum* group have more restricted geographic ranges than members of the former group. *Ptychohyla schmidtorum schmidtorum* occurs on the Pacific slopes of the Sierra Madre in Chiapas and Guatemala, where it occurs with *P. euthysanota euthysanota; P. schmidtorum chamulae* is known from only two localities on the Atlantic slopes of the Central Highlands of Chiapas, where it occurs close to, but as now known not with, *P. euthysanota macrotympanum.* On the Atlantic slopes of the Sierra Madre Oriental in northern Oaxaca *P. ignicolor* occurs with *P. leonhardschultzei.*

In the Sierra de los Tuxtlas in southern Veracruz and in the cloud forests along the eastern slopes of the Sierra Madre Oriental northward to Nuevo León, *Hyla miotympanum* seems to be the ecological replacement of *Ptychohyla.* On the Pacific slopes north of Guerrero, México, humid forests in which there are cascading mountain streams are absent; consequently, no *Ptychohyla* are known from that region. In the mountains of El Salvador *Ptychohyla euthysanota euthysanota* occurs sympatrically with another small stream-breeding hylid, *Hyla salvadorensis.* To the south of Honduras the highlands diminish into the lowlands of Nicaragua, where habitat suitable for *Ptychohyla* apparently does not exist. In the mountains of Costa Rica and Panamá, the habitats occupied by *Ptychohyla* in northern Central America are filled by a variety of

stream-breeding *Hyla,* such as *Hyla legleri, H. rivularis, H. rufioculis, H. alleei,* and *H. uranochroa.*

Although members of the genus *Ptychohyla* occur in the southern part of the Mexican Highlands to the west of the Isthmus of Tehuantepec, the greater distribution and differentiation in the genus is in the Chiapan-Guatemalan Highlands. In this respect *Ptychohyla* is a counterpart of *Plectrohyla.*

Habitat Preference

Frogs of the genus *Ptychohyla* are ecologically associated with mountain streams at elevations between 650 and 2200 meters; in the geographic region where these frogs occur the vegetation between those elevations consists of cloud forest or pine-oak forest. In some places the frogs have been found in a mixture of oak and semi-deciduous scrub forest. At Vista Hermosa, Oaxaca, *P. leonhardschultzei* and *P. ignicolor* were found in cloud forest, whereas at Agua del Obispo, Guerrero, the former species was found in pine-oak forest. *Ptychohyla schmidtorum* is known only from cloud forest; *P. euthysanota euthysanota* and *P. spinipollex* generally are found in cloud forest, but in some places they live in pine-oak forest. *Ptychohyla euthysanota macrotympanum* has been found in pine-oak forest and in a mixture of oak and semi-deciduous scrub forest. With the possible exception of the members of the *Ptychohyla schmidtorum* group, which has been found only in cloud forest, it seems as though the type of vegetation is not the controlling factor in the ecological distribution of these frogs.

Ptychohyla has been found only where there are clear, cascading streams overhung by vegetation, on which adults and young perch at night, or even by day. The presence of these streams, in which the tadpoles live, seems to be an important factor in the distribution of *Ptychohyla.* As has been shown previously, the tadpoles of *Ptychohyla* are adapted for existence in torrential streams, where the water is cool, and the amount of oxygen is high. Clearly these tadpoles are unsuited for life in ponds or sluggish streams in the lowlands, where the temperature of the water is high, a layer of silt on the bottom is deep, and the amount of oxygen is low. The tadpoles cling to rocks on the bottom of the streams; there they move slowly across the rocks, apparently feeding on the thin covering of algae. Tadpoles were not observed on rocks having a thick covering of algae or moss. The tadpoles were observed to swim against the current in torrential streams, in which no fishes were

found. Therefore, it seems as though the presence of the stream-habitat for the tadpoles is a significant factor in the ecological distribution of the species of *Ptychohyla.*

Interspecific Competition

At localities where two species of *Ptychohyla* occur sympatrically (*P. ignicolor* and *P. leonhardschultzei* at Vista Hermosa, Oaxaca, and *P. euthysanota euthysanota* and *P. schmidtorum schmidtorum* at Finca La Paz, Depto. San Marcos, Guatemala) effort was made to determine what, if any, ecological interspecific relationships existed. Although adults of the sympatric species were found on adjacent leaves or branches of bushes overhanging the streams at both localities, segregation at the time of breeding seems to be maintained by the notably different breeding calls in sympatric species (see discussion of breeding calls). Thus, as has been shown by Blair (1956), Fouquette (1960), and others working on a variety of pond-breeding frogs and toads, the breeding call in *Ptychohyla* acts as an important reproductive isolating mechanism.

At no locality were *Ptychohyla* and associated species of hylids found so abundantly as were species of pond-breeding hylids in the lowlands. Apparently reproductive activity is not concentrated in a short breeding season, and it is highly doubtful if the populations of these frogs are as large as those of the lowland pond-breeders. The continual humid conditions and abundance of insect food throughout the year in the cloud forest are perhaps indicative of little interspecific competition among adults of *Ptychohyla* and other sympatric hylids.

At Finca La Paz, Guatemala, tadpoles of two species of *Ptychohyla* were ecologically segregated. The tadpoles of *P. euthysanota euthysanota* were found in riffles in the streams, whereas those of *P. schmidtorum schmidtorum* were found in slower water, chiefly in small pools in the streams. At Vista Hermosa, Oaxaca, tadpoles of *P. leonhardschultzei* were found in riffles, and tadpoles of the sympatric *P. ignicolor* were found in a small pool in a stream. Similar ecological relationships were observed for several species of Costa Rican hylids. Throughout the range of *Ptychohyla* east of the Isthmus of Tehuantepec, members of the genus occur with species of *Plectrohyla,* all of which are larger than *Ptychohyla,* and all of which have tadpoles that live in torrential streams. Tadpoles of *Ptychohyla spinipollex* have been found in streams inhabited by the tadpoles of *Plectrohyla guatemalensis* and *P. quecchi;* tadpoles of *Ptychohyla euthysanota euthysanota* and *P. schmidtorum schmid-*

torum were found in streams inhabited by tadpoles of *Plectrohyla guatemalensis, P. matudai,* and *P. sagorum.* In some streams great numbers of tadpoles occur. The habitat is rather restricted, and the food supply is limited. Consequently, interspecific competition among the various species of hylids whose tadpoles live in the torrential streams probably is highest during the larval stage. Unfortunately, this aspect of salientian population ecology has received no intensive study.

Reproduction and Development

Since the cloud forests inhabited by *Ptychohyla* are daily bathed in clouds and have a fairly evenly distributed rainfall throughout the year, the frogs living in these forests are active throughout the year. At least some of the species evidently have a long breeding season, for I found calling males of *P. leonhardschultzei* in February, March, and August, and found tadpoles in February, March, June, and August. Tadpoles of the various species have been obtained throughout much of the year, as follows: *P. euthysanota euthysanota,* February, March, May, and July; *P. euthysanota macrotympanum,* March, June, and August; *P. spinipollex,* February, March, April, June, July, and August; *P. schmidtorum schmidtorum,* March, May, June, July, and August; *P. schmidtorum chamulae,* June and August; *P. ignicolor,* June. I suspect that this temporal distribution more accurately reflects the seasonal activities of collectors than of the frogs.

Calling frogs usually are on vegetation adjacent to or overhanging streams; some calling males of *P. spinipollex* were on rocks in or by streams. Clasping pairs of *P. euthysanota* and *P. schmidtorum* were observed on vegetation by streams. Despite intensive search, no eggs were found. It is doubtful if *Ptychohyla* deposit eggs on vegetation overhanging streams, as do centrolenids and *Phyllomedusa,* for egg-clutches of these frogs are easily found. Possibly the eggs are laid separately on vegetation above the stream, in which case they could be overlooked easily. In streams where *Ptychohyla* and other hylid tadpoles occur, empty egg capsules have been found on the lee sides of rocks, but there is no way to determine which species laid the eggs.

Numbers of eggs were counted in gravid females; the largest eggs have diameters ranging from 2.5 to 3.0 mm. The smaller species, comprising the *Ptychohyla schmidtorum* group, have fewer eggs than do the larger species. Numbers of eggs found in females of the various species are: *P. euthysanota euthysanota,* 108; *P. euthy-*

sanota macrotympanum, 136, 160; *P. leonhardschultzei,* 141; *P. spinipollex,* 119, 134, 143; *P. schmidtorum schmidtorum,* 59, 61, 90; *P. schmidtorum chamulae,* 60, 71, 89.

Duration of the larval stage is unknown. Metamorphosing young have been found from May through August. From two to six completely metamorphosed young are available for each of the species, except for *P. ignicolor* of which none is available. The smallest young frog is a *P. euthysanota* having a snout-vent length of 14.2 mm.; the largest young frog is a *P. schmidtorum schmidtorum* having a snout-vent length of 17.0 mm.

PHYLOGENY OF PTYCHOHYLA

The preceding data on morphology, life histories, and behavior form the basis for the following interpretation of the phylogeny of *Ptychohyla.* Additional data are needed to support some of the ideas discussed below; many of the data that are available for *Ptychohyla* are lacking for other, possibly related, hylids. The family Hylidae is composed of several hundred species, and most of the species are poorly known. Consequently, any attempt to place *Ptychohyla* in the over-all scheme of hylid phylogeny would be premature at this time. But, as between the five species of two species-groups here recognized as constituting the genus *Ptychohyla,* some estimate of relationships can be made. First, it is necessary to determine the validity of the genus itself.

Ptychohyla as a Natural Assemblage

As stated in the diagnosis of the genus, the only character that sets this group of species apart from other hylids is the presence of ventrolateral glands in the breeding males. To many systematists the thought of being able to identify to genus only breeding males is sufficiently disturbing to cause them to view with disfavor the recognition of the genus. Nonetheless, the question is raised: Do the five species herein placed in the genus *Ptychohyla* constitute a natural assemblage? If the genus is considered to be more than a category of convenience, that is to say, a group of related species having a common origin, the primary problem is to determine whether or not the five species form a phylogenetic unit.

The species of *Ptychohyla* are divided into two groups on the basis of external morphology, breeding calls, and tadpoles. The *Ptychohyla euthysanota* group seems to be a natural group composed of three species, all of which are more closely related to one another than to any other hylid. Likewise, the species comprising

the *Ptychohyla schmidtorum* group seem to represent a natural unit. If the presence of ventrolateral glands in breeding males is ignored, a student of salientian systematics might derive the *Ptychohyla euthysanota* group from a hylid stock containing *Hyla miotympanum* and *Hyla mixomaculata.* Likewise, *Ptychohyla schmidtorum* could be placed with *Hyla uranochroa* and related species in Costa Rica. Nonetheless, the fact remains that all of the species assigned to the genus *Ptychohyla* have ventrolateral glands in the breeding males; furthermore, ventrolateral glands are unknown in other hylids. If the *P. schmidtorum* group and the *P. euthysanota* group each evolved from separate hylid stocks, then the ventrolateral glands must have developed independently in both groups. That ventrolateral glands developed independently in five species of frogs in southern México and northern Central America and not in any of the other approximately 500 species of hylids in the world is untenable. It is more logical to assume that the development of the glands took place only once in a stock of hylids that gave rise to the five species herein recognized as members of the genus *Ptychohyla.*

Generic Relationships

The affinities of *Ptychohyla* apparently are not with any of the other groups that have been generically separated from *Hyla.* Of the daughter genera in Middle America only *Plectrohyla* has stream-adapted tadpoles, but these large frogs are not closely related to *Ptychohyla.* Stuart (1954:169) suggested that certain montane species of *Hyla* in lower Central America and *Hyla salvadorensis* in El Salvador may be related to *Ptychohyla* or even congeneric. I have had experience with most of these species in the field and believe that Stuart was correct in his suggestion of relationships. The species concerned are four red-eyed stream-breeding *Hyla* in Costa Rica—*H. alleei, H. legleri, H. rufioculis,* and *H. uranochroa,* plus *Hyla salvadorensis* in the mountains of El Salvador. Morphologically all of the species are similar; *Hyla uranochroa, H. legleri,* and *H. rufioculis* have a lateral white stripe that is expanded to form a spot beneath the eye, as in *Ptychohyla schmidtorum.* The tadpoles of *Hyla rufioculis* and *H. uranochroa* have large funnel-shaped mouths and long slender tails like those of *Ptychohyla schmidtorum.* Lips of the tadpoles of *H. legleri* and *H. salvadorensis* are folded laterally, in this respect resembling those of the *Ptychohyla euthysanota* group. I do not know the tadpoles and the breeding call of *Hyla alleei.* The breeding calls of *Hyla rufioculis*

and *H. uranochroa* consist of high melodious notes; the calls of *H. legleri* and *H. salvadorensis* consist of series of short notes that have the general characteristics of the call of *Ptychohyla schmidtorum*. Affinities of the genus *Ptychohyla* seem to me to be with the red-eyed species forming the *Hyla uranochroa* group in Costa Rica. All of the species in the *Hyla uranochroa* group have large frontoparietal fontanelles, rather small ethmoids, and small nasals that are not in contact with one another or with the ethmoid. Some species have a complete quadratojugal-maxillary arch; others do not. Assuming that the parental stock that gave rise both to the *Hyla uranochroa* group and to *Ptychohyla* was widespread in Central America at a time of cooler, more humid conditions, it is possible that with subsequent warming temperatures and seasonal rainfall in the lowlands the parental stock was restricted to the Costa Rican highlands, where the *Hyla uranochroa* group developed, and to the Chiapas-Guatemala highlands, where *Ptychohyla* evolved.

Interspecific Relationships

Ptychohyla schmidtorum is thought to resemble more closely the parental stock of the genus than does any other species of *Ptychohyla* now extant. This parental stock is discussed above in the account of the generic relationships. *Ptychohyla schmidtorum* has a red eye, white lateral stripe, frontoparietal fontanelle, funnel-shaped mouth in tadpoles, and lacks nuptial spines; in all of these characters it resembles members of the *Hyla uranochroa* group. Probably during times of glaciation during the Pleistocene, when climates in México and Central America were depressed, the *Ptychohyla* stock was more widespread than it is now. Subsequent elevation of climatic zones during interglacial periods would have isolated populations as they are today in regions of cloud forests. Thus, through geographic isolation populations could have differentiated and evolved into the present species. Climatic fluctuation in the Pleistocene must have been of sufficient magnitude to permit the spread of cool, moist forests containing *Ptychohyla* across the Isthmus of Tehuantepec into the mountains of Oaxaca.

Because of its small nuptial spines, small triangular vomers, coloration, and absence of a rostral keel, *Ptychohyla euthysanota*, more than any of the other species in the *P. euthysanota* group, resembles *P. schmidtorum*. At the present time *P. euthysanota* and *P. schmidtorum* are sympatric.

As I have mentioned previously, ecological segregation and in-

terspecific competition probably is highly developed in the tadpoles of *Ptychohyla.* If this ecological segregation resulted from intraspecific competition in a stock of *Ptychohyla,* possibly *P. euthysanota* and *P. schmidtorum* differentiated sympatrically in this way. Specific identity is maintained, at least in part, by different breeding calls in males.

Ptychohyla spinipollex and *P. leonhardschultzei* seem to be more closely related to one another than either is to *P. euthysanota.* Probably a stock of *P. euthysanota* was isolated on the Atlantic slopes of northern Central America from *P. euthysanota* on the southern slopes. The frogs on the Atlantic slopes differentiated and spread into the mountains of Oaxaca, where through isolation by the barrier of the Isthmus of Tehuantepec they developed into *P. leonhardschultzei,* while the stock on the northern slopes of Central America evolved into *P. spinipollex.* Subsequent to the differentiation of *P. leonhardschultzei* and *P. spinipollex* from *P. euthysanota* and during a time of cooler more equable climate than exists now, *P. euthysanota* and *P. schmidtorum* invaded the Central Highlands of Chiapas. Subsequent climatic changes isolated populations of each in the Central Highlands, where *P. euthysanota macrotympanum* and *P. schmidtorum chamulae* evolved. *Ptychohyla ignicolor* probably represents stock of *P. schmidtorum* that crossed the Isthmus of Tehuantepec and became isolated in Oaxaca on the western side of the isthmus.

LITERATURE CITED

AHL, E.
1934. Über eine sammlung von Reptilien und Amphibien aus Mexiko, Zool. Anz., 106:184-186, April 15.

BLAIR, W. F.
1956. Call difference as an isolation mechanism in southwestern toads (genus *Bufo*). Texas Jour. Sci., 8:87-106, March.

DUELLMAN, W. E.
1956. The frogs of the hylid genus *Phrynohyas* Fitzinger, 1843. Misc. Publ. Mus. Zool. Univ. Michigan, 96:1-47, pls. 1-6, February 21.
1960. Synonymy, variation, and distribution of *Ptychohyla leonhardschultzei* Ahl. Studies of American Hylid Frogs, IV. Herpetologica, 16:191-197, September 23.
1961. Descriptions of two species of frogs, genus Ptychohyla. Studies of American Hylid Frogs, V. Univ. Kansas Publ. Mus. Nat. Hist., 13:349-357, pl. 25, April 27.

FOUQUETTE, M. J.
1960. Isolating mechanisms in three sympatric treefrogs in the Canal Zone. Evolution, 14:484-497, December.

KELLOGG, R.
1928. An apparently new *Hyla* from El Salvador. Proc. Biol. Soc. Washington, 41:123-124, June 29.

MERTENS, R.
1952. Die Amphibien und Reptilien von El Salvador. Senckenbergischen Naturf. Gesell., 487:1-120, pls. 1-16, December 1.

RIDGWAY, R.
1912. Color standards and color nomenclature. Washington, D. C., 44 pp., 53 pls.

SHANNON, F. A.
1951. Notes on a herpetological collection from Oaxaca and other localities in Mexico. Proc. U. S. Nat. Mus., 101:465-484, May 17.

STUART, L. C.
1954. Descriptions of some new amphibians and reptiles from Guatemala. Proc. Biol. Soc. Washington, 67:159-178, August 5.

TANNER, W. W.
1957. Notes on a collection of amphibians and reptiles from southern Mexico, with a description of a new *Hyla*. Great Basin Nat., 17:52-56, July 31.

TAYLOR, E. H.
1937. New species of hylid frogs from Mexico with comments on the rare *Hyla bistincta* Cope. Proc. Biol. Soc. Washington, 50:43-54, pls. 2-3, April 21.
1942. New tailless amphibia from Mexico. Univ. Kansas Sci. Bull., 28: 67-89, May 15.
1944. A new genus and species of Mexican frogs. Univ. Kansas Sci. Bull., 30:41-45, June 12.
1949. New or unusual Mexican amphibians. Amer. Mus. Novitates, 1437:1-21, December 7.

Transmitted December 27, 1962.

29-6531

(Continued from inside of front cover)

18. Conspecificity of two pocket mice, Perognathus goldmani and P. artus. By E. Raymond Hall and Marilyn Bailey Ogilvie. Pp. 513-518, 1 map. January 14, 1960.
19. Records of harvest mice, Reithrodontomys, from Central America, with description of a new subspecies from Nicaragua. By Sydney Anderson and J. Knox Jones, Jr. Pp. 519-529. January 14, 1960.
20. Small carnivores from San Josecito Cave (Pleistocene), Nuevo León, México. By E. Raymond Hall. Pp. 531-538, 1 figure in text. January 14, 1960.
21. Pleistocene pocket gophers from San Josecito Cave, Nuevo León, México. By Robert J. Russell. Pp. 539-548, 1 figure in text. January 14, 1960.
22. Review of the insectivores of Korea. By J. Knox Jones, Jr., and David H. Johnson. Pp. 549-578. February 23, 1960.
23. Speciation and evolution of the pygmy mice, genus Baimoys. By Robert L. Packard. Pp. 579-670, 4 plates, 12 figures in text. June 16, 1960.

Index. Pp. 671-690

Vol. 10. 1. Studies of birds killed in nocturnal migration. By Harrison B. Tordoff and Robert M. Mengel. Pp. 1-44, 6 figures in text, 2 tables. September 12, 1956.
2. Comparative breeding behavior of Ammospiza caudacuta and A. maritima. By Glen E. Woolfenden. Pp. 45-75, 6 plates, 1 figure. December 20, 1956.
3. The forest habitat of the University of Kansas Natural History Reservation. By Henry S. Fitch and Ronald R. McGregor. Pp. 77-127, 2 plates, 7 figures in text, 4 tables. December 31, 1956.
4. Aspects of reproduction and development in the prairie vole (Microtus ochrogaster). By Henry S. Fitch. Pp. 129-161, 8 figures in text, 4 tables. December 19, 1957.
5. Birds found on the Arctic slope of northern Alaska. By James W. Bee. Pp. 163-211, plates 9-10, 1 figure in text. March 12, 1958.
*6. The wood rats of Colorado: distribution and ecology. By Robert B. Finley, Jr. Pp. 213-552, 34 plates, 8 figures in text, 35 tables. November 7, 1958.
7. Home ranges and movements of the eastern cottontail in Kansas. By Donald W. Janes. Pp. 553-572, 4 plates, 3 figures in text. May 4, 1959.
8. Natural history of the salamander, Aneides hardyi. By Richard F. Johnston and Gerhard A. Schad. Pp. 573-585. October 8, 1959.
9. A new subspecies of lizard, Cnemidophorus sacki, from Michoacán, México. By William E. Duellman. Pp. 587-598, 2 figures in text. May 2, 1960.
10. A taxonomic study of the middle American snake, Pituophis deppei. By William E. Duellman. Pp. 599-610, 1 plate, 1 figure in text. May 2, 1960.

Index. Pp. 611-626.

Vol. 11. Nos. 1-10 and index. Pp. 1-703, 1958-1960.

Vol. 12. 1. Functional morphology of three bats: Sumops, Myotis, Macrotus. By Terry A. Vaughan. Pp. 1-153, 4 plates, 24 figures in text. July 8, 1959.
*2. The ancestry of modern Amphibia: a review of the evidence. By Theodore H. Eaton, Jr. Pp. 155-180, 10 figures in text. July 10, 1959.
3. The baculum in microtine rodents. By Sydney Anderson. Pp. 181-216, 49 figures in text. February 19, 1960.
*4. A new order of fishlike Amphibia from the Pennsylvanian of Kansas. By Theodore H. Eaton, Jr., and Peggy Lou Stewart. Pp. 217-240, 12 figures in text. May 2, 1960.
5. Natural history of the bell vireo. By Jon C. Barlow. Pp. 241-296, 6 figures in text. March 7, 1962.
6. Two new pelycosaurs from the lower Permian of Oklahoma. By Richard C. Fox. Pp. 297-307, 6 figures in text. May 21, 1962.
7. Vertebrates from the barrier island of Tamaulipas, México. By Robert K. Selander, Richard F. Johnston, B. J. Wilks, and Gerald G. Raun. Pp. 309-345, pls. 5-8. June 18, 1962.
8. Teeth of Edestid sharks. By Theodore H. Eaton, Jr. Pp. 347-362, 10 figures in text. October 1, 1962.

More numbers will appear in volume 12.

Vol. 13. 1. Five natural hybrid combinations in minnows (Cyprinidae). By Frank B. Cross and W. L. Minckley. Pp. 1-18. June 1, 1960.
2. A distributional study of the amphibians of the Isthmus of Tehuantepec, México. By William E. Duellman. Pp. 19-72, pls. 1-8, 3 figures in text. August 16, 1960.
3. A new subspecies of the slider turtle (Pseudemys scripta) from Coahulia, México. By John M. Legler. Pp. 73-84, pls. 9-12, 3 figures in text. August 16, 1960.
4. Autecology of the copperhead. By Henry S. Fitch. Pp. 85-288, pls. 13-20, 26 figures in text. November 30, 1960.
5. Occurrence of the garter snake, Thamnophis sirtalis, in the Great Plains and Rocky Mountains. By Henry S. Fitch and T. Paul Maslin. Pp. 289-308, 4 figures in text. February 10, 1961.
6. Fishes of the Wakarusa river in Kansas. By James E. Deacon and Artie L. Metcalf. Pp. 309-322, 1 figure in text. February 10, 1961.
7. Geographic variation in the North American cyprinid fish, Hybopsis gracilis. By Leonard J. Olund and Frank B. Cross. Pp. 323-348, pls. 21-24, 2 figures in text. February 10, 1961.

(Continued on outside of back cover)

(Continued from inside of back cover)

8. Decriptions of two species of frogs, genus Ptychohyla; studies of American hylid frogs, V. By William E. Duellman. Pp. 349-357, pl. 25, 2 figures in text. April 27, 1961.
9. Fish populations, following a drought, in the Neosho and Marais des Cygnes rivers of Kansas. By James Everett Deacon. Pp. 359-427, pls. 26-30, 3 figs. August 11, 1961.
10. Recent soft-shelled turtles of North America (family Trionychidae). By Robert G. Webb. Pp. 429-611, pls. 31-54, 24 figures in text. February 16, 1962.

Index. Pp. 613-624.

Vol. 14. 1. Neotropical bats from western México. By Sydney Anderson. Pp. 1-8. October 24, 1960.
2. Geographic variation in the harvest mouse. Reithrodontomys megalotis, on the central Great Plains and in adjacent regions. By J. Knox Jones, Jr., and B. Mursaloglu. Pp. 9-27, 1 figure in text. July 24, 1961.
3. Mammals of Mesa Verde National Park, Colorado. By Sydney Anderson. Pp. 29-67, pls. 1 and 2, 3 figures in text. July 24, 1961.
4. A new subspecies of the black myotis (bat) from eastern Mexico. By E. Raymond Hall anad Ticul Alvarez. Pp. 69-72, 1 figure in text. December 29, 1961.
5. North American yellow bats, "Dasypterus," and a list of the named kinds of the genus Lasiurus Gray. By E. Raymond Hall and J. Knox Jones, Jr. Pp. 73-98, 4 figures in text. December 29, 1961.
6. Natural history of the brush mouse (Peromyscus boylii) in Kansas with description of a new subspecies. By Charles A. Long. Pp. 99-111, 1 figure in text. December 29, 1961.
7. Taxonomic status of some mice of the Peromyscus boylii group in eastern Mexico, with description of a new subspecies. By Ticul Alvarez. Pp. 113-120, 1 figure in text. December 29, 1961.
8. A new subspecies of ground squirrel (Spermophilus spilosoma) from Tamaulipas, Mexico. By Ticul Alvarez. Pp. 121-124. March 7, 1962.
9. Taxonomic status of the free-tailed bat, Tadarida yucatanica Miller. By J. Knox Jones, Jr., and Ticul Alvarez. Pp. 125-133, 1 figure in text. March 7, 1962.
10. A new doglike carnivore, genus Cynaretus, from the Clarendonian Pliocene, of Texas. By E. Raymond Hall and Walter W. Dalquest. Pp. 135-138, 2 figures in text. April 30, 1962.
11. A new subspecies of wood rat (Neotoma) from northeastern Mexico. By Ticul Alvarez. Pp. 139-143. April 30, 1962.
12. Noteworthy mammals from Sinaloa, Mexico. By J. Knox Jones, Jr., Ticul Alvarez, and M. Raymond Lee. Pp. 145-159, 1 figure in text. May 18, 1962.
13. A new bat (Myotis) from Mexico. By E. Raymond Hall. Pp. 161-164, 1 figure in text. May 21, 1962.
14. The mammals of Veracruz. By E. Raymond Hall anad Walter W. Dalquest. Pp. 165-362, 2 figures. May 20, 1963.
15. The recent mammals of Tamaulipas, México. By Ticul Alvarez. Pp. 363-473, 5 figures in text. May 20, 1963.

More numbers will appear in volume 14.

Vol. 15. 1. The amphibians and reptiles of Michoacán, México. By William E. Duellman. Pp. 1-148, pls. 1-6, 11 figures in text. December 20, 1961.
2. Some reptiles and amphibians from Korea. By Robert G. Webb, J. Knox Jones, Jr., and George W. Byers. Pp. 149-173. January 31, 1962.
3. A new species of frog (Genus Tomodactylus) from western México. By Robert G. Webb. Pp. 175-181, 1 figure in text. March 7, 1962.
4. Type specimens of amphibians and reptiles in the Museum of Natural History, the University of Kansas. By William E. Duellman and Barbara Berg. Pp. 183-204. October 26, 1962.
5. Amphibians and Reptiles of the Rainforests of Southern El Petén, Guatemala. By William E. Duellman. Pp. 205-249, pls. 7-10, 6 figures in text. October 4, 1963.
6. A revision of snakes of the genus Conophis (Family Colubridae, from Middle America). By John Wellman. Pp. 251-295, 9 figures in text. October 4, 1963.
7. A review of the Middle American tree frogs of the genus Ptychohyla. By William E. Duellman. Pp. 297-349, pls. 11-18, 7 figures in text. October 18, 1963.

More numbers will appear in volume 15.

LIBRARY
HARVARD UNIVERSITY

UNIVERSITY OF KANSAS PUBLICATIONS
MUSEUM OF NATURAL HISTORY

Volume 15, No. 8, pp. 351-468, pls. 19-22, 20 figs.
December 30, 1963

Natural History of the Racer Coluber constrictor

BY

HENRY S. FITCH

UNIVERSITY OF KANSAS
LAWRENCE
1963

UNIVERSITY OF KANSAS PUBLICATIONS
MUSEUM OF NATURAL HISTORY

Institutional libraries interested in publications exchange may obtain this series by addressing the Exchange Librarian, University of Kansas Library, Lawrence, Kansas. Copies for individuals, persons working in a particular field of study, may be obtained by addressing instead the Museum of Natural History, University of Kansas, Lawrence, Kansas. There is no provision for sale of this series by the University Library, which meets institutional requests, or by the Museum of Natural History, which meets the requests of individuals. Nevertheless, when individuals request copies from the Museum, 25 cents should be included, for each separate number that is 100 pages or more in length, for the purpose of defraying the costs of wrapping and mailing.

* An asterisk designates those numbers of which the Museum's supply (not the Library's supply) is exhausted. Numbers published to date, in this series, are as follows:

Vol. 1. Nos. 1-26 and index. Pp. 1-638, 1946-1950.

*Vol. 2. (Complete) Mammals of Washington. By Walter W. Dalquest. Pp. 1-444, 140 figures in text. April 9, 1948.

Vol. 3. *1. The avifauna of Micronesia, its origin, evolution, and distribution. By Rollin H. Baker. Pp. 1-359, 16 figures in text. June 12, 1951.
*2. A quantitative study of the nocturnal migration of birds. By George H. Lowery, Jr. Pp. 361-472, 47 figures in text. June 29, 1951.
3. Phylogeny of the waxwings and allied birds. By M. Dale Arvey. Pp. 473-530, 49 figures in text, 13 tables. October 10, 1951.
*4. Birds from the state of Veracruz, Mexico. By George H. Lowery, Jr., and Walter W. Dalquest. Pp. 531-649, 7 figures in text, 2 tables. October 10, 1951.
Index. Pp. 651-681.

*Vol. 4. (Complete) American weasels. By E. Raymond Hall. Pp. 1-466, 41 plates, 31 figures in text. December 27, 1951.

Vol. 5. Nos. 1-37 and index. Pp. 1-676, 1951-1953.

*Vol. 6. (Complete) Mammals of Utah, *taxonomy and distribution*. By Stephen D. Durrant. Pp. 1-549, 91 figures in text, 30 tables. August 10, 1952.

Vol. 7. Nos. 1-15 and index. Pp. 1-651, 1952-1955.

Vol. 8. Nos. 1-10 and index. Pp. 1-675, 1954-1956.

Vol. 9. *1. Speciation of the wandering shrew. By James S. Findley. Pp. 1-68, 18 figures in text. December 10, 1955.
2. Additional records and extension of ranges of mammals from Utah. By Stephen D. Durrant, M. Raymond Lee, and Richard M. Hansen. Pp. 69-80. December 10, 1955.
3. A new long-eared myotis (Myotis evotis) from northeastern Mexico. By Rollin H. Baker and Howard J. Stains. Pp. 81-84. December 10, 1955.
4. Subspeciation in the meadow mouse, Microtus pennsylvanicus, in Wyoming By Sydney Anderson. Pp. 85-104, 2 figures in text. May 10, 1956.
5. The condylarth genus Ellipsodon. By Robert W. Wilson. Pp. 105-116, 6 figures in text. May 19, 1956.
6. Additional remains of the multituberculate genus Eucosmodon. By Robert W. Wilson. Pp. 117-123, 10 figures in text. May 19, 1956.
7. Mammals of Coahuila, Mexico. By Rollin H. Baker. Pp. 125-335, 75 figures in text. June 15, 1956.
8. Comments on the taxonomic status of Apodemus peninsulae, with description of a new subspecies from North China. By J. Knox Jones, Jr. Pp. 337-346, 1 figure in text, 1 table. August 15, 1956.
9. Extensions of known ranges of Mexican bats. By Sydney Anderson. Pp. 347-351. August 15, 1956.
10. A new bat (Genus Leptonycteris) from Coahulia. By Howard J. Stains. Pp. 353-356. January 21, 1957.
11. A new species of pocket gopher (Genus Pappogeomys) from Jalisco, Mexico. By Robert J. Russell. Pp. 357-361. January 21, 1957.
12. Geographic variation in the pocket gopher, Thomomys bottae, in Colorado. By Phillip M. Youngman. Pp. 363-387, 7 figures in text. February 21, 1958.
13. New bog lemming (genus Synaptomys) from Nebraska. By J. Knox Jones, Jr. Pp. 385-388. May 12, 1958.
14. Pleistocene bats from San Josecito Cave, Nuevo León, México. By J. Knox Jones, Jr. Pp. 389-396. December 19, 1958.
15. New subspecies of the rodent Baiomys from Central America. By Robert L. Packard. Pp. 397-404. December 19, 1958.
16. Mammals of the Grand Mesa, Colorado. By Sydney Anderson. Pp. 405-414, 1 figure in text, May 20, 1959.
17. Distribution, variation, and relationships of the montane vole, Microtus montanus. By Sydney Anderson. Pp. 415-511, 12 figures in text, 2 tables. August 1, 1959.

(Continued on inside of back cover)

LIBRARY
JUL 21 1964
HARVARD
UNIVERSITY

UNIVERSITY OF KANSAS PUBLICATIONS
MUSEUM OF NATURAL HISTORY

Volume 15, No. 8, pp. 351-468, pls. 19-22, 20 figs.
December 30, 1963

Natural History of the Racer Coluber constrictor

BY

HENRY S. FITCH

UNIVERSITY OF KANSAS
LAWRENCE
1963

University of Kansas Publications, Museum of Natural History
Editors: E. Raymond Hall, Chairman, Henry S. Fitch,
Theodore H. Eaton, Jr.

Volume 15, No. 8, pp. 351-468, pls. 19-22, 20 figs.
Published December 30, 1963

University of Kansas
Lawrence, Kansas

PRINTED BY
JEAN M. NEIBARGER, STATE PRINTER
TOPEKA, KANSAS
1963

29-7864

Natural History of the Racer Coluber constrictor

BY

HENRY S. FITCH

CONTENTS

PAGE

INTRODUCTION 355
ACKNOWLEDGMENTS 357
METHODS AND MATERIALS 358
DESCRIPTION 362
  Color pattern 362
  Bodily proportions 365
  Lepidosis 367
  Dentition 369
  Hemipenis 369
RELATIONSHIPS 370
RANGE 371
GEOGRAPHIC VARIATION 373
HABITAT 375
TEMPERATURE RELATIONSHIPS 377
HOME RANGE AND MOVEMENTS 385
FOOD HABITS 394
  Methods of obtaining prey 394
  Composition of food 395
  Kinds of prey 403
REPRODUCTION 408
  Sexual behavior 408
  Cycle of the male 414
  Eggs 416
  Hatching 423
GROWTH 425
MORTALITY FACTORS AND ADAPTATIONS FOR SURVIVAL 432
  Defense and escape 432
  Natural enemies 438
  Disease 442
  Parasites 442

PAGE
Populations 445
Composition 445
Numbers 450
Summary 456
Literature Cited 461

Introduction

Throughout much of the United States the racer is abundant and is one of the snakes best known to man. Its active diurnal habits and its preference for a habitat in meadows, pastures, and hayfields rather than in remote wilderness areas, result in frequent encounters with humans. The racer is a predator on many kinds of small animals, both vertebrates and invertebrates; it takes as food chiefly animals that are agricultural pests but also destroys some beneficial kinds. Yet, in general, the attitudes of rural people toward the racer are little influenced by these economic and ecologic considerations, but rather, are dominated by an unreasonable fear, despite the racer's inoffensive disposition, and inability to inflict any harm on humans.

Although an extensive literature exists regarding the racer, no thorough study of the species' natural history has been made heretofore. Obviously such study is needed. Few species of vertebrates having comparable economic bearing have been similarly neglected. In 1948, undertaking a program of ecological research on the recently created University of Kansas Natural History Reservation, I included the racer among the many common species studied to gain insight into the functioning of the local ecosystem. Live-trapping of snakes on the area was begun in 1949, and these operations were greatly intensified in the years 1957 through 1962, with efforts concentrated on the study of the racer in the 1960, 1961 and 1962 seasons. Thus my study is based upon 14 consecutive years' records on the Reservation, the northeasternmost section in Douglas County, Kansas, six and one-half miles north northeast of the University of Kansas campus at Lawrence. After the acquisition in 1956 of the 160-acre Rockefeller Tract adjacent to the Reservation on the north in Jefferson County, field work was extended to this new area, which, because it was superior habitat, in the final years of the study produced more records than the Reservation. An important but relatively minor segment of the data originated from Harvey County Park, 13 miles west of Newton, Kansas, where lines of live-traps were maintained in 1959, 1960, 1961, 1962. Smaller collections of data were obtained from the Lalouette Ranch in the Flint Hills, three miles northeast of Florence, Marion County, Kansas, and from Cedar Bluff Reservoir, 23 miles west and seven miles south of Hays in Trego County, western Kansas, where live-trapping was carried on in 1959 and 1960. Additional data were

obtained on numerous field trips to various collecting localities in northeastern Kansas. My first-hand knowledge of the species is also based, in part, on many years of field experience with the far western subspecies *C. c. mormon* in western Oregon and California, and on similar experience in 1947 and 1948 with the southern subspecies, *C. c. anthicus* in central Louisiana.

This varied field experience with the species at localities well scattered throughout its geographic range has added perspective to the study even though most of the records were collected within a radius of three quarters of a mile. No one locality can be regarded as entirely typical of a species' habitat over its range as a whole. According to my philosophy, the ecological niche of a species is subject to geographical variation analogous to the variation to be seen in the morphological characters of the animal itself. Different community associates, including different competitors, prey, and predators, and different physical factors enforce a somewhat different way of life on a species in geographically remote parts of its range. When analyzed these differences often turn out to have a genetic basis. Thus, limits of tolerance to heat, cold, and drought often vary geographically, and the population density, reproductive potential, seasonal cycle, and other properties of populations may be altered either by the direct effect of the environment, or through its effect on the genetic constitution, produced by natural selection.

The local population of racers studied was near the center of the species' geographic range, and is to some extent representative of the species as a whole, though differing in its ecology from other populations in proportion to their remoteness and the distinctness of their habitats. It has not been demonstrated that ecological traits of populations change in a discontinuous manner or correspond in their limits with those of named subspecies. More likely geographical variation is continuous and parallels morphological variation only in a general way. Certainly the boundaries of subspecies' ranges should not be accorded undue emphasis in an ecological study.

My investigation of the blue racer under natural conditions, combined with a compilation and analysis of published literature, has resulted in a fairly satisfactory understanding of some phases of the species' ecology and natural history, such as the food habits, the growth rate, the extent of home range and of seasonal movements. However, relatively little was learned concerning some phases of

the life history. Unfortunately, the traps used did not catch young of the smaller sizes. Facts concerning egg-laying, incubation, and hatching therefore are known chiefly from snakes kept in confinement. Although first-year young were captured by hand from time to time they were obtained in relatively small numbers, and little was learned regarding their population density, movements, or mortality factors. Of course, such hiatuses are to be expected; even in man such enigmas as the disparate sex ratio still challenge the investigator.

For the subspecies of racer involved in my field study the widely used vernacular "blue racer" has been adopted in this report. In general I advocate conformity with the vernacular names published by the Committee on Herpetological Common Names (1956). However, in this list, the name blue racer was assigned to *Coluber constrictor foxi*, an invalid subspecies of the Prairie Peninsula that has been relegated (Auffenberg, 1955:92; Smith, 1961:196) to the synonymy of *C. c. flaviventris*. It therefore seems appropriate that the book name "yellow-bellied racer" applied to *flaviventris* by the Committee should be abandoned for this subspecies, and that the name blue racer be applied officially, as it is in actual practice by both laymen and herpetologists, to all populations of this subspecies.

Acknowledgments

Financial assistance from the National Science Foundation in 1957 through 1962 is acknowledged. Although none of the three separate grants involved was made specifically for the autecological study of the racer, all three contributed to the support of the extensive program of live-trapping for snakes, which yielded most of the records upon which this report is based. Student assistants who were employed on these projects include James W. Bee, William N. Berg, Donna M. Hardy, Robert M. Hedrick, Dale Hoyt, Robert M. Packard, Robert G. Webb, and Wayne Wiens, at the Reservation; Roy Henry, Dale Horst, Dwight R. Platt, and Howard L. Schrag at Harvey County Park, and Gilbert L. Adrian at Cedar Bluff Reservoir. Dr. Edwin P. Martin, formerly of Fort Hays, Kansas State College, was helpful in planning and carrying out the field work at Cedar Bluff Reservoir. Eric Shulenberger assisted with field work and processing of data in 1962 under the National Science Foundation program for Undergraduate Research Participation. Robert Miner assisted with the examination of specimens in 1960. Mr. August Lalouette of Florence, Kansas, permitted field

work on his ranch and contributed information and materials to expedite this work. Mr. and Mrs. Harold Brune of Route 3, Lawrence, Kansas, kindly contributed several clutches of racer eggs found on their farm in Jefferson County, and also made available significant information accompanying them. Dr. William H. Stickel kindly made available at my request records of predation on racers from the food habits files of the U. S. Fish and Wildlife Service. Dr. William E. Duellman of the University of Kansas Museum of Natural History and Dr. Robert C. Stebbins of the University of California Museum of Vertebrate Zoology kindly permitted examination and dissection of specimens in the collections under their care. Dr. George W. Byers of the University of Kansas Department of Entomology identified numerous insects eaten by racers. My daughter, Alice V. Fitch, often assisted me with the field work and the processing of data. My wife, Virginia R. Fitch, read the manuscript critically, assisted me with the examination of museum specimens, and with typing, and helped in various other ways.

Methods and Materials

This investigation was based primarily on the capture in live-traps, marking, release, and recapture of blue racers in their natural habitat. On the combined area of the Reservation and the Rocke-

TABLE 1. NUMBERS AND DISTRIBUTION OF CAPTURES AND RECAPTURES OF BLUE RACERS ON THE RESERVATION AND ROCKEFELLER TRACT

Span of years within which each individual was captured		Number of separate years within which each individual was captured		Number of times each individual was captured	
Years	Individuals	Years	Individuals	Times captured	Individuals
1	749	1	749	1	679
2	137	2	197	2	181
3	56	3	51	3	93
4	32	4	15	4	31
5	19	5	6	5	7
6	13	6	1	6	14
7	7	7	0	7	8
8	2	8	1	8	4
9	3			9	1
10	0			10	0
11	1			11	0
12	1			12	1
				13	0
				14	0
				15	0
				16	1

feller Experimental Tract, 1020 blue racers were recorded a total of 1688 times from August 30, 1948, to October 27, 1962. At Harvey County Park 361 blue racers were marked, and were captured a total of 467 times from May 6, 1959, to September 14, 1962, and at Cedar Bluff Reservoir 42 were captured from May 11, 1959, to June 30, 1960.

The traps used were cylinders of galvanized wire, "hardware cloth" (Fitch, 1951:77; 1960:77), having funnels opening into each end, or having a funnel at one end and a plug at the other. The traps, open at both ends, were used along hilltop rock ledges where an exposed vertical rock face provided a barrier along which a snake might travel and where it could be easily intercepted by the trap without any accessory equipment (see Pl. 21, Fig. 1). Where such natural barriers were lacking, as in level fields, barriers consisting of boards, screens or sheet metal were installed to guide the racer toward the trap and into a funnel entrance. Two such barriers at each end of a trap forming a V to guide the snake into the funnel were used in 1956 and 1957, when trapping at places away from the hibernation ledges was undertaken. Later it was found simpler and more effective to use a single barrier with a trap at each end. The barrier extended up into the funnel entrance, and usually the racer, following along the barrier on either side, would pass into the funnel and through its apex. However, it was possible for a racer to travel around the end of the barrier without entering the trap, and perhaps some did so.

The need for making the barrier and trap a tight unit impassable to the snake, was somewhat counterbalanced by the need for having the whole installation loosely constructed so that it could be easily altered, opened, adjusted, and cleaned. Since the traps were kept set in large numbers, and the task of checking them was time-consuming, speed of operation was more important than the perfect functioning of any one trap. Approximately 200 traps were kept set when operations were at their maximum. No record was kept of the number of "trap days" involved in the study, but the total was well over 100,000 for the Reservation and the Rockefeller Tract. When traps were set at both ends of a barrier, the outer end of each trap was closed with a plug. No bait was used in the traps. Occasionally small vertebrates and insects of kinds used as food by the racers may have gotten caught first and served to attract the snakes. Best catches of racers were made in the breeding season, since males were attracted by females already in the traps, and

several males might be captured simultaneously with one female. Occasionally as a person approached or handled a trap, a racer darted out of it, displaying a perception, acuity of vision, and skill in avoiding the inward projecting wire prongs encircling the small funnel opening, that were exceptional among the several species of snakes trapped. Doubtless many other racers that were caught in traps escaped before they were discovered. If the funnel entrance of the trap was of the same diameter as the snake itself, or only a little larger, there was little likelihood of the trapped racer escaping. However, funnel openings were usually adjusted at a diameter of approximately 1¼ inches, allowing an ample margin for even the largest racers, though inadequately small to permit ingress of a few of the largest black rat snakes, bull snakes and timber rattlers occurring locally.

Ordinarily the snakes trapped were processed in the field and released immediately. The method of marking was essentially that of Blanchard and Finster (1933:334). Two subcaudals, one on the right side and one on the left, were clipped on each snake, and when these marks healed they left permanent scars. In the racer, as in most other colubrines, the subcaudals are divided into a double series, one on the left and one on the right. Scales of the left and right sides are placed alternately. At the base of the tail one or more undersized scales usually are present on each side, and there might be some question as to precisely where the count should begin. The rule followed was to exclude from the count any small basal scales on either side that did not extend medially to contact at least one scale of the opposite side. The scale designated as "one left" (or "one right") was the first to contact one of the opposite series, regardless of whether the former was of normal size or (as was usually the case) smaller and narrower than those following it. In marking, this "number one" scale was never clipped but was left as a point of reference since a base mark was needed from which to begin the count. The marks were read from left to right, for example U 5*l* 2*r*, the "U" referring to the subcaudals or "urosteges," the "5*l*" indicating the fifth on the left side, and "2*r*" indicating the second on the right. The subcaudals clipped were the first 19 following the basal scale. When the 361 possible combinations all had been used, ending with U 20*l* 20*r*, a new series was begun duplicating the first except that on each snake the first ventral (or "gastrostege") anterior to the anal plate was clipped on the left side (G1L) to distinguish these snakes from the series

previously marked. Later, a third series, "G2R" was marked, and eventually a fourth series, "G3L" was started.

There were many borderline instances in which the basal scale barely contacted one of the opposite side. In such instances the formula was written U $5l_{ISB}$ $2r$, the subscript ISB signifying "including small basal." In other instances a basal subcaudal barely failed to contact a scale of the opposite side and this condition was indicated by the subscript NSB—"not including small basal." The condition might be so nearly equivocal that on successive occasions the same formula might be read U $5l_{ISB}$ $2r$ and U $4l_{NSB}$ $2r$. Occasional misidentifications of individuals that resulted from such discrepancies were in most instances readily detected when the field records were transferred to individual file cards where the sex, size, and location of the snake at its previous captures were shown.

In some instances racers recaptured after periods of years retained conspicuous scars where scales had been clipped, but in other instances the marks had become obscure, and in fact the only trace of a mark might be a slight narrowing or notching of part of the scale originally clipped. Snakes caught and marked early in life probably retained more power of regeneration than those clipped after the attainment of maturity, but otherwise the basis for difference in extent of regeneration was not evident. In the same snake, three scales, all clipped on the same day, might show much different degrees of regeneration after the lapse of a year or more. In general, obscuring of marks by regeneration was a source of inconvenience rather than of error; only a negligible percentage of the recaptured racers had marks so obscure that their identities might have been seriously questioned, and it is doubtful that any marks were lost completely by regeneration.

Racers found in traps were removed, measured (snout-to-vent length, tail length), weighed in a cloth bag suspended from spring scales, and marked. The mouth was forced open and the snake was examined for flukes. Enamel paint of a bright color, red, green, yellow, blue or orange was smeared on the snake to gain information regarding the time of molt. The stomach was palpated for recently ingested food items, and any detected were forced up into the gullet to be identified, then were squeezed back into the stomach. The rear part of the body was palpated to detect undigested material in the gut, and if any was present, an attempt was made to squeeze out the fecal material, using only light pres-

sure, with care not to injure the racer. The inside of the trap and the ground beneath it were inspected for fecal material that might have been voided while the snake was confined. Any scatological material obtained was wrapped in a paper towel, labelled and brought back to the laboratory where it was stored. Eventually each scat was soaked for a day or more in a detergent solution, rinsed in running water in a fine gauze bag, dried, and placed with its label in a cellophane envelope for subsequent microscopical study.

Various items concerning reproductive condition were also routinely recorded. In females the ventral surface was palpated at the rear end of the body to detect the genital bursa or vagina, which in sexually mature individuals has a much thickened wall, and can be felt as a distinct lump. Males were likewise tested for sexual maturity by pipetting a small amount of fluid from the cloaca into a vial and returning it to the laboratory where it was examined microscopically for motile sperm. Also, sperm samples were often taken from males at different times throughout the season of activity, and cloacal samples from females occasionally were checked for sperm as evidence of recent copulation.

In the summer of 1962 an outdoor enclosure of 100-foot circumference was constructed, of galvanized sheet iron, with wall three feet high, set on a concrete base extending to a depth of two feet. A two-foot-deep concrete basin inside the enclosure served as a water container. The enclosure was partly shaded by a large walnut tree and the area enclosed had lush vegetation, including brome grass, various shrubs, and young trees up to 15 feet high, thus including most features of the racers' habitat, and it was situated in an area frequented by the snakes. Throughout the summer several racers were kept in the enclosure, and frequent observations on them yielded much information concerning time of activity, temperature preferences, and social and sexual behavior that could not have been obtained readily either from racers confined in small cages or from those free under natural conditions.

Description

Color Pattern

Hatchling racers differ much in appearance from adults; whereas the latter are of dull uniform coloration dorsally, the hatchlings have a checkered pattern of alternating blotches in several rows, including a middorsal row, with blotches much larger than those of

the other rows. This basic pattern is perhaps the most common one in all snakes, and is found in the young of various other genera (notably *Elaphe*) which lose or alter their markings during development. In these genera and in the racer, the juvenal checkered pattern may represent recapitulation of an ancestral condition. The adaptive significance of having a blotched, checkered pattern in the young, and uniform coloration in the adult is not evident. I have rarely seen the hatchlings under natural conditions except by finding them hiding beneath flat rocks. Their concealing pattern must be fully as effective as that of adults and the young themselves are more secretive than the adults.

A hatchling of 240 millimeters snout-vent length was described as follows on September 22, 1962: Ground color pale olive anteriorly, gradually darkening posteriorly, marked with chocolate blotches; middorsal blotches largest averaging about five scales long and seven or eight scales wide anteriorly; posteriorly, blotches become less distinct (tending to blend into progressively darkening ground color), and width-to-length ratio increases; gradual obscuring of blotches proceeds posteriorly, until on tail they can no longer be distinguished, and color is uniformly olive; on each side, row of lateral blotches alternates with that of middorsal blotches; lateral blotches average somewhat less than two scales long, and approximately two scales wide and are of irregular shape, sometimes subdivided; farther down on sides, lower row of lateral blotches alternates with upper lateral row; this lower lateral row, approximately same size as upper lateral row, and situated at level of first scale row, overlapping onto ventrals, where it pales to reddish brown; almost every ventral scute has one pair or more of dark reddish brown spots, tending toward semicircular shape, the arc of each projecting forward, but posteriorly on body these spots become increasingly obscure, and are indiscernible on posterior end of body and on tail; ventral surface white on chin and throat, gradually assuming suffusion of pale greenish gray posteriorly; eye dark with narrow yellowish margin around pupil; top of head grayish olive, mottled with faint and irregular dark markings; supralabials whitish, with chocolate markings, mostly wedge-shaped, in their posterior parts; rostral and internasals edged with dark posteriorly; posterior upper corner of loreal and adjacent corner of prefrontal dark; temporals having dark markings; chin almost immaculate, but with narrow black posterior edges on some of the infralabials (see Plate 19, Figs. 1 and 2, and Plate 20, Fig. 2).

The checkered pattern of the juvenile fades gradually as development proceeds. Persistence of the juvenal markings varies greatly in individuals and probably is subject to geographic variation also. By the time sexual maturity is attained the dorsal pattern often is indiscernible or represented only by faint traces. The ventral speckling is more persistent.

A female of 602 millimeters snout-vent length in mid-July 1962, at a probable age of 11 months, was described as follows: Overall dorsal color olive gray, but with remnants of juvenal pattern discernible; dark dorsal blotches have almost faded, but their edges, about one scale wide, are still distinct; low on sides, color fades to pale bluish gray, and to pale greenish blue on edges of ventrals; on anterior one-third of body midventral surface is lemon yellow; farther posteriorly it fades to ivory, almost white on tail; chin white, except for reddish brown posterior edges of last infralabials, and streak of same color on each antepenultimate infralabial; top of head olive gray with irregular scattered dark marks; preoculars pale centrally with olive brown edges; supralabials white with reddish brown triangular marks; postnasals white anteriorly, gray posteriorly; uppermost postocular brownish orange, paler centrally; two rows of semicircular spots on belly, distinct anteriorly, but fading posteriorly until indiscernible on posterior part of belly; numerous small black spots scattered irregularly over dorsal and lateral surfaces.

A male racer retained more of the juvenal pattern at an approximate age of 15 months, when he was described on November 30, 1961: Dorsal surface dark grayish brown, the large juvenal dorsal blotches (each about eight scales wide) easily discernible, but faint; top of head dark olive brown, mottled with black, paling in rostral region; supralabials white on their anterior and lower portions, marked with brown and blue-gray on their upper and posterior portions; chin white, but with rusty markings on last four infralabials; ventrals ivory-yellow with rusty spots of which the largest are approximately three-fourths of the ventrals' breadth; first row of scales bluish gray, or with greenish suffusion (in neck), most of scales having indistinct dark spots; second row of scales similarly colored but more suffused with dusky pigment, blending into the darker duller color of the dorsal surface.

A female of 720 millimeters snout-vent length, presumably about 20 months old, but not gravid, on June 13, 1962, was described as follows: Juvenal pattern no longer clearly discernible but scattered

traces of it remain; dorsal color predominantly grayish olive, with occasional small black spots in streaks scattered irregularly over dorsal and lateral surfaces; at anterior end of body lateral scales have bluish green edges but this shading becomes less noticeable posteriorly; head mostly olive dorsally with marking obscure; parietals have a large faint blotch; supralabials retain faint dark, brownish markings on their upper parts; dark spot on median edge of each prefrontal; supraoculars slightly darker than adjacent scutes; chin mostly white, with yellowish suffusion at edges of scales; ventral surface predominantly yellow, but fading to grayish white posteriorly; remnants of juvenal ventral spots faintly discernible as tan or whitish areas on yellow ventrals.

Munro (1950b:124) mentioned a blue racer of 749 millimeters total length (hence probably having a snout-vent length of 600 millimeters, or a little less), which retained faint juvenal markings when caught on June 23, 1948, even though it was sexually mature, since it laid eggs on the night of July 4, 1948. During several weeks of captivity this snake's markings faded perceptibly.

In fully adult blue racers, those more than three years old, the juvenal markings have become completely obliterated. In those from the area of my study, the dorsal coloration is subject to much individual variation, typically olive brown, but ranging from pale bluish gray to dark brown, dark blue, or slaty. In most, the dorsal color is uniform, but in some there are streaks and isolated scales of black. The dark dorsal color extends down the sides onto the lateral corners of the ventrals and the subcaudals. The chin is white but the remainder of the ventral surface is ivory colored.

Bodily Proportions

The slender and streamlined bodily proportions of the racer are subject to change through allometric growth. The head, and especially the eyes, are relatively large in the hatchling, and become relatively smaller as growth proceeds. The relative tail length seemingly increases in the growing young and then decreases slightly in adults.

Snout-vent length and tail length were recorded in almost all the racers examined, but other measurements were recorded in relatively few. In many racers, especially the larger adults, tails had been damaged and lacked their terminal parts. Often only the tip was missing, but, of course, such individuals were not usable in the study of proportions of the tail. Table 2 summarizes information concerning relative tail length in 935 racers of both sexes and

various sizes, from northeastern Kansas. Nearly all measurements are from the live snakes; a few are from recently killed individuals.

In hatchlings, the proportions of the tail are not noticeably different in males and females, but data indicate that the snakes' tails are approximately seven per cent longer in males than in females; as growth proceeds, the tails become relatively longer in proportion to the body, in both sexes. The ratio reaches its maximum in young adults, having increased from approximately 28 per cent of the snout-vent length in males and 26 per cent in females, to 31 per cent in males and a little more than 28 per cent in females. In the largest racers, of both sexes, these percentages are slightly reduced. Tail-length is subject to a fairly wide range of individual variation, which tends to obscure the trends determined by sex and size.

TABLE 2. RELATIVE TAIL LENGTH IN MALE AND FEMALE RACERS OF DIFFERENT SIZE GROUPS

SNOUT-VENT LENGTH IN MILLIMETERS	Males		Females	
	Number of racers	Mean ratio of tail-length to snout-vent length	Number of racers	Mean ratio of tail-length to snout-vent length
150–200	7	27.3±.833	2	26.3
201–250	24	27.8±.490	23	25.9± .479
251–300	9	28.8±.634	4	26.6
301–350	20	29.8±.246	11	25.0±1.060
351–400	8	28.8±.530	12	27.5± .404
401–450	6	27.8±.775	5	26.3± .357
451–500	12	29.7±.434	6	26.8± .858
501–550	45	30.5±.283	15	27.6± .284
551–600	76	31.0±.218	35	27.1± .254
601–650	45	29.6±.313	64	27.8± .163
651–700	50	30.5±.241	36	27.1± .350
701–750	72	30.5±.177	45	27.6± .373
751–800	45	30.3±.373	38	27.8± .325
801–850	48	29.7±.274	50	27.5± .205
851–900	18	29.1±.519	35	28.6± .422
901–950	5	29.8±.672	31	26.7± .252
951–1000....	1	29.5	19	26.9± .390
1001–1050....	.....	.....	15	25.9± .413
1051–1100....	.....	.....	6	26.4± .725
1101–1150....	.....	.....	1	28.5
1151–1200....	.....	.....	1	25.0

In 88 racers caught in the summer of 1962 the following measurements were recorded: Head length, from tip of snout to angle of jaw; maximum head width; greatest diameter of eye; circumference of neck; circumference at mid-body; circumference at posterior end

TABLE 3. BODILY PROPORTIONS (EXPRESSED AS RATIO OF SNOUT-VENT LENGTH) IN RACERS OF DIFFERENT SIZES

SIZE GROUP	Large (more than 800 millimeters)	Medium (500 to 800 millimeters)	Small (less than 500 millimeters)
Length of head	3.61 ± .036	3.82 ± .025	5.39
Width of head	1.93 ± .049	2.02 ± .023	2.53
Diameter of eye	.56 ± .008	.63 ± .009	1.00
Circumference of neck	4.71 ± .082	5.05 ± .052	6.64
Circumference at mid-body	7.11 ± .238	7.66 ± .082	8.58
Circumference at posterior end of body	5.06 ± .113	5.03 ± .061	5.90
Circumference of tail at base	4.23 ± .113 [1] 4.47 ± .171 [2]	4.22 ± .075 [1] 4.66 ± .043 [2]	4.66 [1]

1. Females.
2. Males.

of body; and circumference of tail-base. Because the measurements were small, and were made in the field on active, struggling snakes, a high degree of precision could not be attained, and the range of error was several per cent, with occasional relatively large errors. Nevertheless, ontogenetic trends are clearly indicated. Most of the racers measured were adults of small to medium size—in the range 500 to 799 millimeters, snout-vent length. Twelve females and seven males ranged from 800 to 1035 millimeters, and seven young (all females) were less than 500 millimeters. In measurements other than circumference of tail-base, significant differences could not be found between males and females of the same size group; therefore the sexes were combined to obtain larger series.

Table 3 shows that as compared with adults, the small young racers have stouter, stubbier bodies, relatively large heads, and, especially, large eyes. Allometric growth seems to continue throughout life and the changed proportions of the adults are accentuated in the largest and oldest individuals.

Lepidosis

Scalation that of typical colubrid (see Pl. 19); rostral large, extending back onto dorsal surface of snout, bluntly pointed behind; paired internasals considerably wider than long, convex anteriorly, almost straight-edged posteriorly, each extends laterally to naris;

paired prefontals approximately twice size of internasals, and wider than long, extending laterally on each side to level of nostril; frontal convex anteriorly, concave on each side, bluntly pointed behind, nearly twice as wide anteriorly as posteriorly; parietals large; angle formed between them by frontal slightly more than 90 degrees; nostril large, situated between almost equal sized anterior nasal and posterior nasal plates; loreal slightly smaller than nasals, its anterior edge inclined forward superiorly; two rows of temporals on each side; in upper row, first one narrow and elongate, second much shortened, third intermediate in shape; in lower row all three approximately alike in size and shape; two postoculars, the lower larger; seven supralabials, first small and low, longer along upper edge than along lower, second slightly longer than high, third higher than long, contacting eye; fourth largest, contacting posterior part of eye, and lower postocular; fifth nearly as large, pointed above; sixth also large, pentagonal; seventh low and rectangular; on chin first pair of infralabials separate mental from anterior genials; second infralabial minute; third approximately twice its size; fourth much smaller, rhomboidal, fifth also large, pentagonal; sixth smaller, rhomboidal, bluntly pointed behind; seventh smaller, narrow behind; eighth small and elongate; second pair of genials longer and narrower than those of first pairs, separated from each other by smaller scales; genials in approximately five rows, but somewhat irregular in arrangement, mostly smaller and narrower than body scales; latter all smooth, arranged in 17 rows for about two-thirds of body length, then, by loss of third row on each side, reduced to 15; scales of neck region rounded and relatively small, one-third to one-fourth size of larger body scales; lowest scale row on each side largest with its scales much wider and less symmetrical than others; most of body scales of approximately hexagonal shape; on forebody they average approximately twice as long as wide, but farther posteriorly on body, width-length ratio gradually increases and some of scales, notably those of lowest row, approximately as wide as long; regularity of scale rows broken on sides just above vent by presence of many small additional scales; on tail scale rows drop out posteriorly in rapid succession, until on posterior third only four are present; ventrals strongly convex posteriorly, with free posterior edges, nearly half length of scales; anal plate divided, with diagonal suture; subcaudals in double series, those of right and left sides alternating; several minute subcaudal-like scales on each side of vent.

Dentition

In the racer the maxillary, palatine, pterygoid, and dentary bones bear teeth (Fig. 1). The teeth are all much alike in size and shape, small, sharp, and recurved, typically at an angle of approximately 50 degrees. The number of teeth present is variable. Because the teeth are small and loosely attached to the jaw bones, and often are broken off in the capture and ingestion of prey, each bone usually lacks part of its complement of teeth. Even the sockets vary somewhat in number between individuals, and between the left and right sides in some snakes. Most of the skulls that I examined were not thoroughly cleaned, and the adherent dried tissues made it difficult to obtain accurate counts of the sockets. In ten skulls from Kansas and Nebraska, most frequently occurring numbers of sockets for each of the dentigerous bones were: maxillary, 15; palatine, 11; pterygoid, 18; dentary, 18.

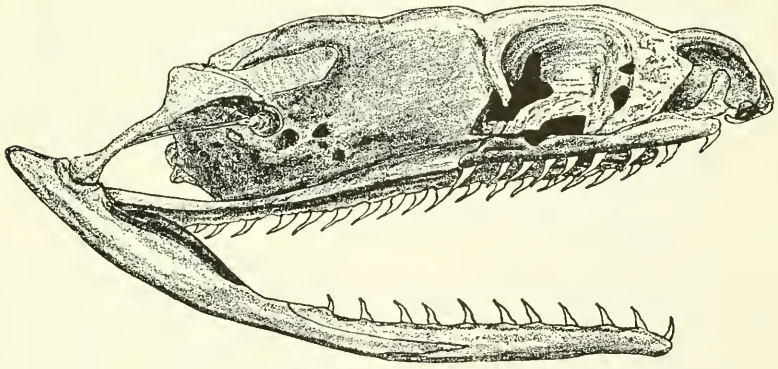


FIG. 1. Lateral view of right side of skull of adult female blue racer, × 4. University of Kansas Museum of Natural History no. 18305, from Greenwood County, Kansas.

Hemipenis

Penial characters have proven to be useful in the classification of snakes, providing bases for separating subfamilies, genera, and species. In the racer even the subspecies have trenchant penial characters by which they may be spearated in some instances. The hemipenis is roughly cylindrical, but widest at the base (Fig. 2). The sulcus spermaticus is unbranched. Approximately the basal one-third of the hemipenis has a smooth surface, broken only by the sulcus spermaticus and by three greatly enlarged spines, which form

hooks—one anterior, one posterior, and one dorsal. The dorsal hook is the largest of the three. Distal to the smooth part is a zone of small spines, each recurved and mounted on a fleshy tubercle. The zone of spines is poorly developed on the anterior side and is interrupted on the posterior side in the vicinity of the sulcus spermaticus but is best developed on the posterior side a short distance above and below the sulcus spermaticus. The spines are arranged in several oblique rows. Those of the proximal row are best developed, and there is rapid diminution in the size of those situated farther distally. Approximately the distal two fifths of the hemipenis forms a third zone, lacking distinct spines, but having numerous deep longitudinal grooves, alternating with lamellae which have fimbriated edges, and which fuse with each other and divide to form a reticulated pattern.

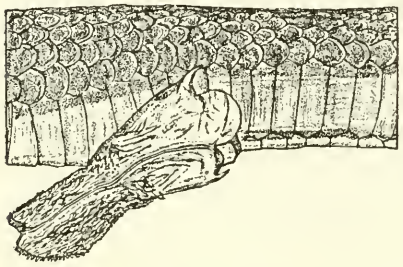


FIG. 2. Lateral view of injected and everted left hemipenis (slightly enlarged) of a blue racer from the Rockefeller Tract, Jefferson County, Kansas, showing heavy spines at base of organ, small spines of central zone and lamellae of terminal part. This hemipenis is not fully engorged.

Relationships

The large genus *Coluber* is much in need of revision. Its many species, perhaps more than a score in all, occur in North America from southern Canada south to Guatemala, in eastern and southwestern Asia, in southern Europe, and in North Africa. All are active, slender-bodied snakes having smooth scales in few rows, and having large eyes with well developed vision. The North American species fall into two natural groups, the typical racers, and the whip snakes, often assigned to a separate genus, *Masticophis* (Ortenburger, 1928). The whip snakes are more specialized than the typical racers in having the eyes more enlarged, and the body form more slender and attenuate, with number of scale rows more reduced. The racers of the Old World are more diverse. Inger and Clark (1943) suggested a partitioning of the genus *Coluber* on the basis of the pattern by which scale rows are reduced, from the maximum number on the forebody to the minimum number at the posterior end of the body, supplemented by certain characters of the hemipenis and of the cephalic scutellation. Besides *Coluber*

and *Masticophis* these authors recognized within the group the genus *Platyceps* with several species in southern Europe and southwestern Asia; *Zamenis* with several species in the same region and in North Africa, and *Haemorrhois,* a monotypic genus of Spain, North Africa and several Mediterranean islands. Although apparently valid in principle, this arrangement has not been generally followed.

Exclusive of those species groups whose assignment to the genus *Coluber* are somewhat questionable, the remaining species in the genus are: *C. constrictor* occurring throughout most of the United States and south along a narrow Atlantic coastal strip of Mexico to Guatemala; *C. oaxacae* of southern Mexico; and *C. spinalis* of northern China. *C. oaxacae* is poorly known as only a few specimens have been collected, but seemingly it is a near relative and derivative of *C. constrictor,* especially of that species' southernmost population. *C. spinalis* is much more distinct, as might be expected from its geographical remoteness. It is a slender, active snake, of olive coloration dorsally with 17 scale rows and a bright yellow, black-edged dorsal stripe and yellow ventral surface. It is relatively small (up to 755 millimeters snout-vent length) and is partial to riparian habitats but is also found in forests and in dry and barren regions (Pope, 1935:224-226). It is known to feed upon lizards.

Range

The common racer has been recorded in each of the 48 states of the mainland of the United States, also in New Brunswick, Nova Scotia, southern British Columbia, and southward through Mexico where it is limited to a narrow strip of east coast lowlands but extends as far as Guatemala. *C. c. constrictor* occupies the northeastern states and extends south into the Appalachian and Piedmont. *C. c. priapus* with its associated races *paludicola, helvigularis,* and *anthicus* has an Austroriparian distribution, occupying the Atlantic Coastal plain and the Gulf Region, and extending north in the Mississippi Valley to southern Illinois and Indiana. *C. c. paludicola* is localized with two disjunct populations—in the Everglades and on Cape Canaveral, Florida. *C. c. helvigularis* is even more restricted in range and is known only from the Appalachicola region of the Florida Panhandle and the adjacent corners of Alabama and Georgia. *C. c. anthicus* occupies much of central and western Louisiana and adjacent Texas. *C. c. flaviventris* occurs throughout the Great Plains, east in the "Prairie Peninsula" through Michigan and northern Ohio and west to the Rocky Mountains. *C. c.*

stejnegerianus occurs from Matagorda Bay in Texas southward through eastern Mexico, with a seemingly isolated population in the Sierra del Carmen region of northern Coahuila. *C. c. mormon* occurs in the Pacific Coast states and Great Basin.

Actually, the range limits and the continuity of distribution within the area outlined are still poorly known. The species has not been recorded from the northern parts of Maine, Vermont, New Hampshire, Michigan, Wisconsin, or Minnesota, nor from northeastern New York. It is generally absent from southwestern desert areas. Records are particularly scarce and scattered in the Rocky Mountain states, suggesting that the distribution in this area may be discontinuous. In a large area comprising all of New Mexico and Arizona, the western half of Colorado, and the southern halves of Utah and Nevada, records are so scarce as to indicate that the species is there represented by only a few well isolated relict colonies. The type locality of *mormon* is "Valley of the Great Salt Lake," and there are numerous records from the northern part of Utah east of Great Salt Lake (Woodbury, 1931:75), but a record from Moab is the only one known to me from the southern half of the state. The only records from western Colorado are from three miles east of Fruita and two miles west of Grand Junction, Mesa County (Maslin, 1959:56). Apparently the only valid record from Arizona is that of Shannon (1950:59) from Eagar, Apache County, in the east-central part. Shannon also recorded the racer from Boulder Dam in extreme southern Nevada. Brattstrom (1955:152) has recorded the species from the lower Pleistocene of southeastern Arizona (Curtis Ranch), bearing out the idea that the racer has partly withdrawn from a range formerly occupied in the Southwest at a time when cooler and moister climate prevailed. Other fossil occurrences are of late Pleistocene age—Vero Beach and Seminole, Florida (Brattstrom, 1953a:245) and, doubtfully, Rancho LaBrea, California (Brattstrom, 1953b:376). The range of *mormon* has been mapped (Wright and Wright, 1949:134) as extending east to south-central Montana on the basis of one specimen allocated on the basis of two characters. Otherwise the range of *mormon* seems to be entirely west of the Continental Divide, well separated from that of *flaviventris* by desert and mountain barriers. The conspecificity of *mormon* with the other subspecies needs to be more thoroughly investigated, and geographic variation within *mormon* also merits study.

Geographic Variation

The common racer and the several species of whip snakes (*Masticophis*) were revised by Ortenburger (1928). More recently with much larger series of specimens, Auffenberg (1955) again revised the classification of *C. constrictor,* but his study was concentrated in Florida and neighboring southeastern states with relatively little attention devoted to populations of the western and central United States. As the species occurs throughout most of the United States and south through the coastal lowlands of eastern Mexico to Guatemala, it is found over a wide range of environmental conditions. Various characters are subject to geographic variation, and some of them follow clines that are maintained over extensive areas. Such characters as the number of hemipenial spines, and the enlargement of one or more basal spines into hooks, the shape of the premaxillary bone, the number of maxillary teeth, the numbers of ventrals and caudals, color of eye, number of dorsal saddle-marks and of ventral spots in juveniles, and ratios of body proportions including tail length to total length have been used to characterize the subspecies.

Also important is the shade of coloration of adults. The subspecies *constrictor, priapus* and *helvigularis* that are characteristic of forested habitats in the eastern United States are black dorsally and have their ventral surfaces suffused to a large extent with dark or dusky coloring. Farther westward the ground color becomes progressively paler, greenish, grayish or light brown, and the ventral surface is yellow (white on the throat and neck). The same tendency appears in *C. c. paludicola* of the Everglades. The populations of arid climates in southern Texas and in the far western states are relatively pale colored. The species thus conforms to Gloger's Rule in changing from a pallid coloration in arid climates to a dark pattern with eumelanins predominating in a humid climate.

Perhaps the most important character that is subject to geographic variation in the racer, and certainly one of the most neglected, is body size. With information now available it is not possible to compare the sizes of different populations except in a general way. The best sources of information concerning size in several subspecies other than *flaviventris,* are the publications of Auffenberg (1949 and 1955). Comparison of these data with my own is not entirely satisfactory because Auffenberg did not indicate clearly differences in size between the sexes, nor indicate the

boundary line between young and adults. Also, his measurements are of overall length. For the purpose of comparison I have subtracted 22.5 per cent, an approximation of ratio of average tail length, from Auffenberg's figures. He stated (1955:98) that the series of specimens on which measurements were based were those "with a uniform coloration," that is to say they had lost the juvenal pattern and were probably sexually mature. Whether the same statement applied to the large series of *stejnegerianus* in the same author's earlier paper (1949:55) is doubtful.

C. c. constrictor: 34 New York specimens averaged 806 millimeters (Auffenberg, 1955:96).

C. c. flaviventris: 100 Kansas specimens averaged 791 millimeters (males, 746; females, 836).

C. c. priapus: 171 Florida specimens averaged 713 millimeters (Auffenberg, 1955:96).

C. c. stejnegerianus: 291 Texas specimens averaged 664 millimeters (Auffenberg, 1949:54).

C. c. mormon: 94 West Coast specimens (Museum of Vertebrate Zoology) averaged 563 millimeters (males 515, females 600).

C. c. anthicus: 35 northern Louisiana specimens estimated to average 582 millimeters (Clark, 1949:249—the author did not present individual measurements, but indicated the numbers in several size groups in his sample).

The 100 *flaviventris* in the above list were recorded in June, July and August, a season when the young of the preceding year are still small, and these young were not included. In a fall sample 63 males averaged 729 millimeters and 65 females averaged 886 millimeters, but with the nearly grown young (44 males and 40 females) included, the averages were changed to 651 and 768 respectively. Maximum length perhaps express differences between the subspecies as well as, or even better than, the averages listed above. The following figures indicate some of the maximum overall length measurements in inches that have been published by various authors. These measurements pertain to females unless otherwise indicated.

C. c. constrictor: 74¾, 74¼, 73, 65½ (Auffenberg, 1955:96).

C. c. flaviventris: 71 (Pope, 1944:172), 72 (Conant, 1958:147).

C. c. priapus: 52½ (♂) (Auffenberg, 1955:98).

C. c. stejnegerianus: 37 (Auffenberg, 1949:54), 40 (Conant, 1958:148).

C. c. mormon: 51½ (Museum of Vertebrate Zoology).

C. c. anthicus: 70 (Conant, 1958:149).

In my own study, the largest racers recorded from the Reservation and Rockefeller Tract had the following overall lengths: 59, 57¼, 55½, 58 ♂ (projected from stub tail).

These sets of figures show that compared with the blue racer in Kansas, with which my own study was concerned, the black racer of the northeastern states reaches a larger size, while the racers of the Southeast and especially those of the far West and of southern Texas, are dwarfed. These size differences are almost certainly correlated with behavioral and ecological differences among the snakes involved. Adaptations to exploit certain types of prey and to utilize most efficiently certain habitats and types of cover, have led to divergent trends in different parts of the range.

Habitat

The racer dwells primarily in open situations, but as might be expected from its extensive geographic range, bringing it under the influence of diverse climates and habitats, its populations have diverged somewhat in adaptation to different environmental conditions. The eastern blacksnakes (subspecies *constrictor* and *priapus*) seem to prefer woodland and forest edge. In central Louisiana, *anthicus* occurs chiefly in an open type of woodland. The subspecies *stejnegerianus* is found chiefly in brushland and thorn forest. The western *mormon* is found in varied habitats, including moist streamside meadows, and chaparral. Published statements of herpetologists, based upon studies in limited areas, are briefly quoted below to show the trend of geographic change.

C. c. constrictor: This snake "occurs chiefly in fields" (Atkinson, 1901:148; Pennsylvania); "in more or less wooded regions and along hillsides and among bushes" (Surface, 1906:167, in Pennsylvania); "abundant, especially in wooded regions" (Hibbard, 1936:28, in Kentucky); "dry and more or less open places" (Conant, 1938:52, in Ohio); "old fields and areas about buildings" (King, 1939:572, in Tennessee).

C. c. priapus: In "drier parts of the [Okefinokee] swamp . . . seems to prefer blueberries and saw palmettos" (Wright and Bishop, 1915:159 in Georgia); "common in grassy fields and in upland woods" (Allen, 1932:13, in Mississippi); "abundant along fence rows . . . in dry pine-oak forest and in bottomland forest" (Trowbridge, 1937:296, in Oklahoma); "probably most abundant in open upland hammock or in old fields; limestone flatwoods" (Carr, 1950:80, in Florida); Oak and oak-hickory forest and small hill prairies in southern Illinois (Rossman, 1960:219).

C. c. paludicola: In "all parts of the freshwater Everglades, in cabbage palm hammocks, in salt marshes, and in mangrove swamps. On Key Largo . . . in mesophytic hammock" (Duellman and Schwartz, 1958:296, in southern Florida).

C. c. anthicus: In "wooded areas in the vicinity of briar patches or other brushy undergrowth" (Clark, 1949:249, in northern Louisiana); "especially grassy uplands" (Fitch, 1949:88, in central Louisiana).

C. c. stejnegerianus: Of 291, 94 were in scattered brush, 92 in sparse brush, 41 in lightly wooded areas, 26 in grassy areas, 24 in heavy brush, eight in semi-arid places and six in heavily wooded situations (Auffenberg, 1949:55, in southern Texas).

C. c. mormon: In "thin brush skirting open prairie land" (Lord, 1866: 304, British Columbia); cottonwood-willow and water margin habitats in prairie (Dice, 1916:310-312, in eastern Washington); "grass; amid water cress; bank of small ditch near meadow; barley field; sandy ground covered with rocks and driftwood; among sedges; in sagebrush; swimming in irrigation ditch" (Grinnell, Dixon and Linsdale, 1930:149, in northeastern California); low foothills, around the fields, and in the timber and brush along the canyon bottoms (Woodbury, 1931:75, in Utah); "open woods of Garry oak and poison oak, on grassy slopes, in chaparral, and in grain or hay fields" (Fitch, 1936:644, in southwestern Oregon); "low hot canyons where it was found to occupy areas having rather dry, rocky hills" (Ferguson, 1952:68, in northeastern Oregon).

C. c. flaviventris: Pastures, meadows, and fields (Hurter, 1911:170, in Missouri); "usually frequents dry open fields, although it is often found in bushes or cut-over land which has grown up into thickets" (Ortenburger, 1928:181); "pasture lands and on hill sides" (Peters, 1942:183, in Illinois); "along the levees in the salt marshes" (Liner, 1954:82, in southern Louisiana); "common in both prairie and woodland habitat" (Smith, 1947:34, in east-central Illinois); Flood plain, sand around sage-sumac brush, rocky slopes (Fouquette and Lindsay, 1955:411, in northwestern Texas).

Several observers have described the habitat in Kansas as follows: "grassy valleys and thinly wooded hillsides" (Burt, 1927:5); "moist and dry habitats, in wooded areas, and in prairies" (Smith, 1956:237); Oak-walnut hillside forest, cultivated field, buckbrush-sumac, prairie (Clarke, 1958:22).

Every part of the 590-acre Reservation is used to some extent by blue racers living on this area. Home ranges of most individuals are so large as to include a variety of habitats, both woodland and grassland. The habitat preferences vary according to season. In autumn some racers migrating to rock ledges to hibernate are found in mesic forest, but at that time of year leaves have begun to fall and the forest floor is less dark and humid than in summer. In spring also racers not yet back on their summer ranges are often seen either along the hilltop ledges, or moving downhill through woods toward bottomland meadows. However, in summer, the finding of a racer in mesic woodland is a rare event. Occasionally the snakes make trips across such blocks of woodland hundreds of feet wide, but they do not linger in the woodland. In decreasing order of preference the habitats used by racers on my study area may be classified as follows:

1. Tall-grass prairie, (Plate 22) either original or regenerated, dominated by native perennial grasses in stands three feet to seven feet high, including big blue-stem (*Andropogon gerardi*), little blue-stem (*A. scoparius*) Indian grass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*).

2. Pastureland, with introduced brome grass (*Bromus inermis*) and associated weedy vegetation.

3. Brush, in ravines, at woodland edge, and in riparian thickets.

4. Weedy fields, dominated by such pioneer plants as ragweeds, sunflowers, horseweed, milkweed, wild lettuce, aster and goldenrod.

5. Open type of woodland dominated by such trees as honey locust and osage orange.

These habitat types are interspersed on the study area, and each racer has a wide choice of habitats without travelling beyond the limits of its own chosen area.

Grassland that has been closely grazed, mowed or burned does not provide entirely adequate food or shelter, and under such conditions clumps of brush or other dense vegetation may be of critical importance. Throughout the racer's extensive range, fields of grain and hay at times provide suitable habitat, and may support large populations, but in spring, before the young cultivated plants have made much growth, or later in the season, after they have been cut, the racer may need to depend on adjacent areas of pasture, thicket, or woodland edge and the availability of such refugia to a large extent determines the numbers of racers on cultivated areas.

Temperature Relationships

In the locality of my study racers spend approximately half the year in winter dormancy. Earliest spring records and latest fall records for 13 years are shown in Table 4. The spring records in nearly all instances pertain to snakes found in the open or beneath flat rocks warmed by sunshine, usually at or near the rock ledges where hibernation occurs. Juveniles are especially well represented in these earliest spring records, and it seems that they tend to emerge a little earlier, on the average, than the adults, either because they have hibernated in more superficial and less well insulated situations or because their lesser body mass permits more rapid warming to activity than can occur in the adults. The latest fall records all pertain to racers trapped along the rock outcrops, and none was a young of the year.

TABLE 4. EARLIEST AND LATEST RECORDED ANNUAL DATES WHEN BLUE RACERS WERE ACTIVE ON THE RESERVATION OR ROCKEFELLER TRACT

YEAR	Earliest spring record	Latest fall record	YEAR	Earliest spring record	Latest fall record
1950.....	April 16	November 4	1957.....	April 30	November 2
1951.....	April 19	November 13	1958.....	April 25	November 20
1952.....	April 23	November 12	1959.....	April 6	November 10
1953.....	April 8	November 12	1960.....	April 22	November 6
1954.....	April 20	November 12	1961.....	April 19	November 1
1955.....	April 15	November 2	1962.....	April 23	October 27
1956.....	May 11	November 14			

Most of the population undoubtedly emerged somewhat later than the average date of April 16 indicated by the records in Table 4, and retired somewhat earlier than the average date of November 8. However, a small percentage of the population probably emerged even earlier each year than my records indicate, and retired into hibernation later than my records indicate. In a typical year, temperatures in April and early May are only occasionally above the level at which racers are able to become active, but are below this threshold most of the time. The same statement applies to an autumn period of late October and November. Most racers are dormant in their hibernacula during these transitional periods of spring and autumn, but some—those that have emerged early in spring, or those that have not yet retired (in fall)—retreat to temporary shelters and revert to a semi-torpid state when temperatures fall below the critical level.

Fig. 3 shows the relative extent of activity along the hilltop outcrops, as reflected by numbers of racers caught at different times during the autumn. Data from 14 years are combined, and the large composite sample indicates that in an average year there is relatively little activity along the hilltop outcrops in early September, but that activity rapidly increases to a peak in mid-October and then tapers off rapidly, usually ending in mid-November, but occasionally ending as early as late October or as late as late November.

The racers recorded in traps had, in many instances, been confined in them for from one to three days before they were found. For any one year records are not sufficiently numerous to show the trend as well as Fig. 3, but Fig. 4 shows year-to-year differences; 1958 was a fairly typical year, and also was the year in which the largest sample was obtained; in 1949 the largest catches were made earlier than usual, and the racers retired early into hibernation; in 1954 warm weather persisted until unusually late in autumn, and racers remained active beyond the time when they ordinarily would have been hibernating; in 1955 and 1961 the most concentrated activity along the outcrops, as reflected by day to day catches, came later than usual, but unseasonably cold weather ended all activity abruptly, earlier than usual.

The racer's annual cycle of activity is, of course, controlled primarily by the weather, and is much delayed or accelerated in some years. But certain stabilizing factors cause the racer's annual cycle to be less variable than that of the weather. For example, in spring

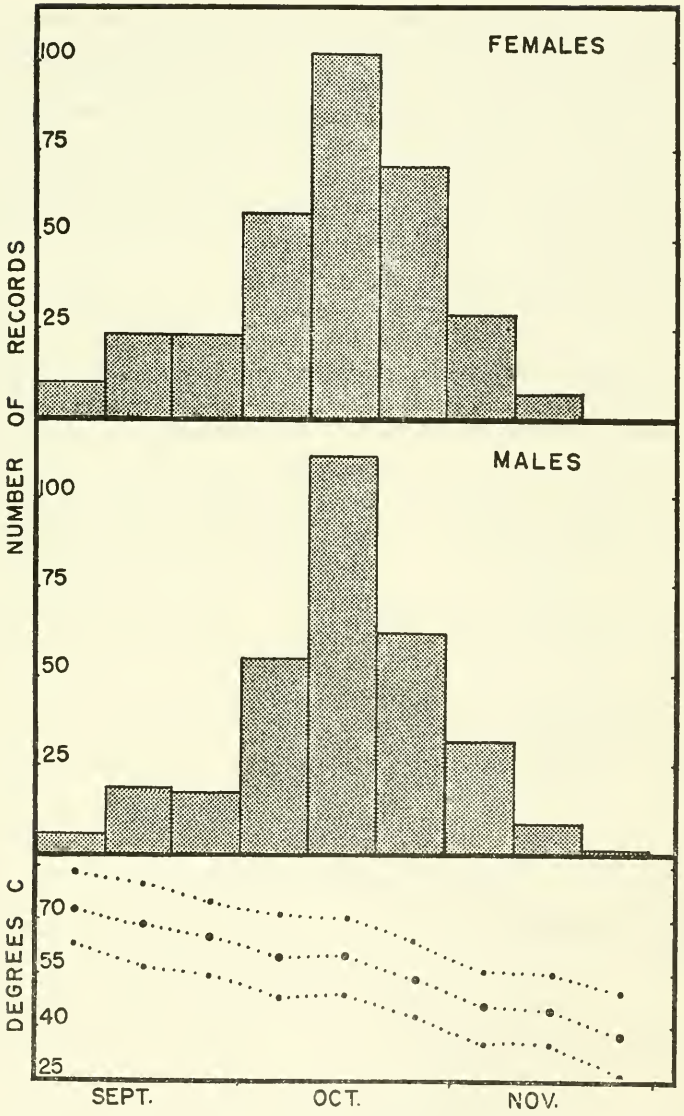


FIG. 3. Records of blue racers trapped along hilltop limestone outcrops in autumn, a composite sample of 14 years (1949 through 1962) from the Reservation and Rockefeller Tract, showing the catch grouped in ten-day intervals, beginning with September 1 to 10 and ending with November 20 to 29. Averages of the maxima, means, and minima of daily temperatures for each period are shown.

when persistently cool weather delays emergence from hibernation beyond the normal time, the increasing azimuth of the sun, and more intense sunshine cause the soil to warm, despite low air temperature, until emergence is finally triggered. Having once emerged, the racer is able to control its bodily temperature to a large extent by basking in sunshine to gain warmth, or by seeking shade or underground shelter to escape overheating. By such behavioral thermoregulation extremes of weather are neutralized, or at least buffered to some degree.

In the course of my study no racers were found in their actual hibernacula. Insofar as known, these were always in deep crevices in strata of limestone near hilltops, and were inaccessible except by removal of the solid rock. The crevices where racers hibernate are known to be several feet deep in some instances, extending well below the frost line. Periodic temperature readings in two such crevices at depths of 12 inches and 30 inches, taken in the winter of 1954 (Fitch, 1956:471) showed that temperatures during dormancy are usually well within the range 0° C to 10°. Whether the

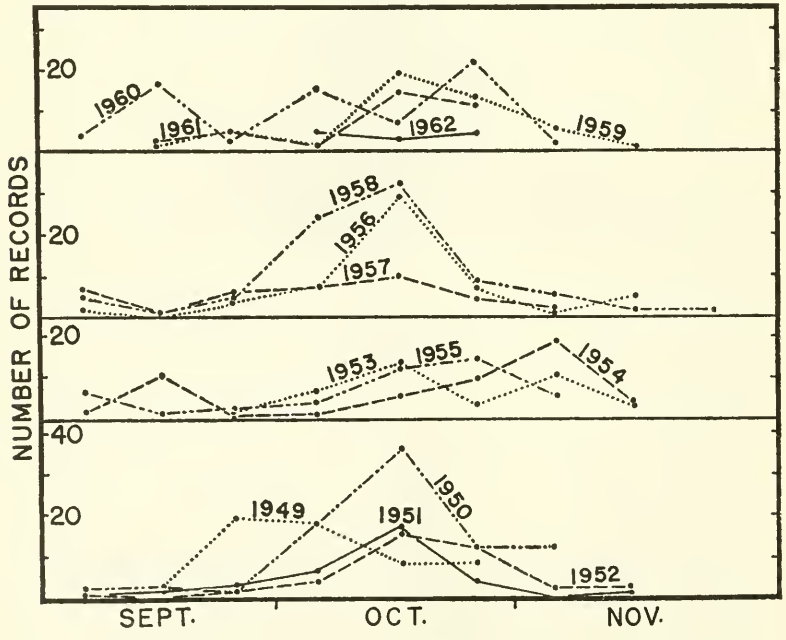


FIG. 4. Yearly variation in catch of blue racers along hilltop outcrop in autumn on the Reservation and Rockefeller Tract, grouped in same ten-day intervals indicated for Fig. 3.

racers congregate in hibernating masses in regular "dens" on the Reservation has not been definitely determined, but if so, most of the hibernating groups must be small, because those trapped along the ledges are well scattered, and, in fact, give the impression of being rather uniformly distributed along them. However, ledges of northward exposure are not used as hibernation sites, so far as known, and those of full southward exposure are perhaps preferred, especially where the hilltop has a southward projecting spur, and the exposed rock face is extensive, with many cracks and fissures. I have been unable to detect differences in types of hibernation sites preferred between the racer and the copperhead, which is somewhat more numerous on the same area.

Several authors have contributed to knowledge of hibernation in the racer. Boyer and Heinze in Missouri (1934:195) noted that blue racers often were associated with copperheads in the vicinity of places chosen for hibernation. Burt (1935:329) in Kansas found blue racers emerging from dens among rocks on a prairie hillside, associating with other snakes, *Diadophis punctatus, Elaphe guttata,* and *Pituophis melanoleucus.* In the Chicago region, Pope (1944: 173) reported scores of blue racers aggregating in October on and around a sand dune with oak woodland. In Ohio, Conant (1938: 55) found three blue racers hibernating together about three feet underground in a small hole. One found at another locality had apparently hibernated in company with a massasauga (*Sistrurus catenatus*). In Maryland Cohen (1939:137) saw racers (*C. c. constrictor*) in the act of emerging from an old vole burrow that was a communal hibernaculum, on April 6, 8, and 10. Air temperatures at the time of emergence were 12.5° and 18.5° Centigrade. In Illinois, Schroder (1950:1-2) found seven blue racers hibernating in masses, intertwined with each other and with bull snakes at depths of 36 inches and 42 inches in an abandoned mammal burrow in a sand dune area in early February.

In the course of routine field work I often carried a Schultheis quick-reading thermometer, and from time to time I had opportunities to take the body temperatures of blue racers newly captured by hand. The trend of these records indicated the temperature range within which the snakes normally limit their activity, and the preferred temperature. In an earlier publication (Fitch, 1956: 459-460) based on a few more than half the number of records of temperature now available, I discussed responses of the blue racer to temperature. The newer data bear out the trends previously

revealed; of 60 records, 39 are within the six-degree range from 29° to 35°, and records are most concentrated in the one-degree range, 34° to 35°. Racers were found active at air temperatures between 15.5° and 32.4°, with the greatest concentration between 26° and 27°. Compared with most other kinds of North American snakes, the racer is remarkably tolerant of heat, and often is several degrees warmer than the level that those of other genera will normally tolerate. Racers have been seen crawling in the sunshine, or basking on days that were uncomfortably hot for humans. For example, on August 28, a large female racer released from a trap was followed and her behavior observed; after crawling some 50 feet through the grass she climbed from a ditch bank onto sunflower stalks and elm saplings, and came to rest among the stalks,

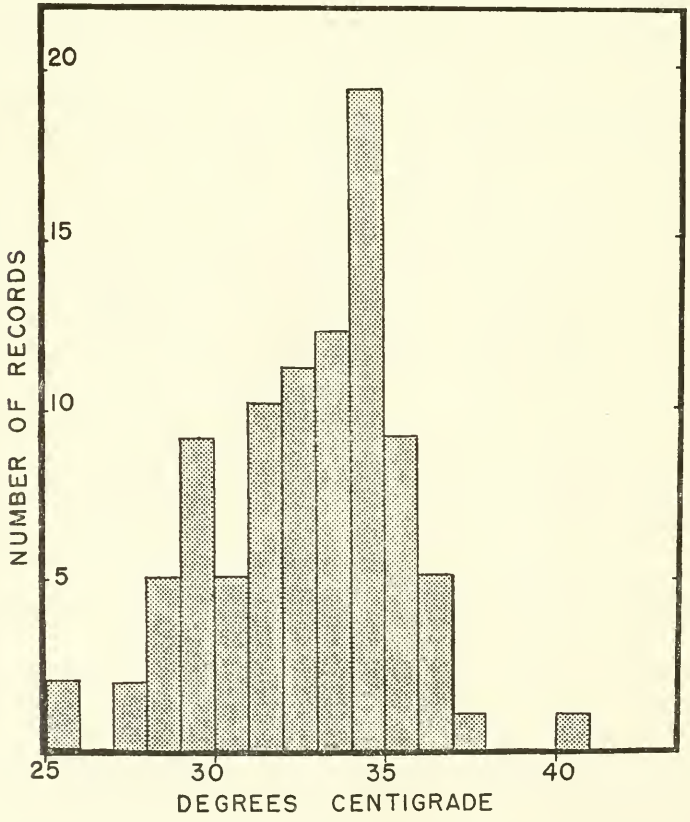


FIG. 5. Bodily temperatures of blue racers kept in a large outdoor enclosure and checked from time to time when they were active and the sun was shining, in June and July, 1962.

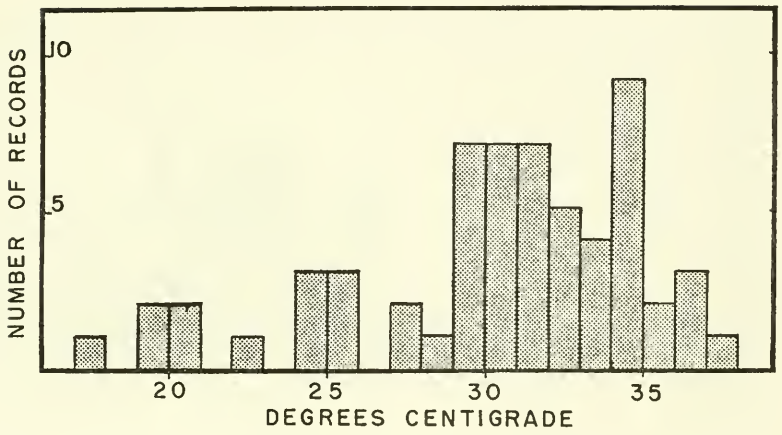


FIG. 6. Bodily temperatures of blue racers captured by hand in their natural surroundings. The preferred level is approximately the same as indicated by Fig. 5 (between 29° and 36° Centigrade), but some of the racers caught were not fully active and had lower temperatures. Some bias results from the fact that those having the lowest temperatures were the least active and hence were most easily caught.

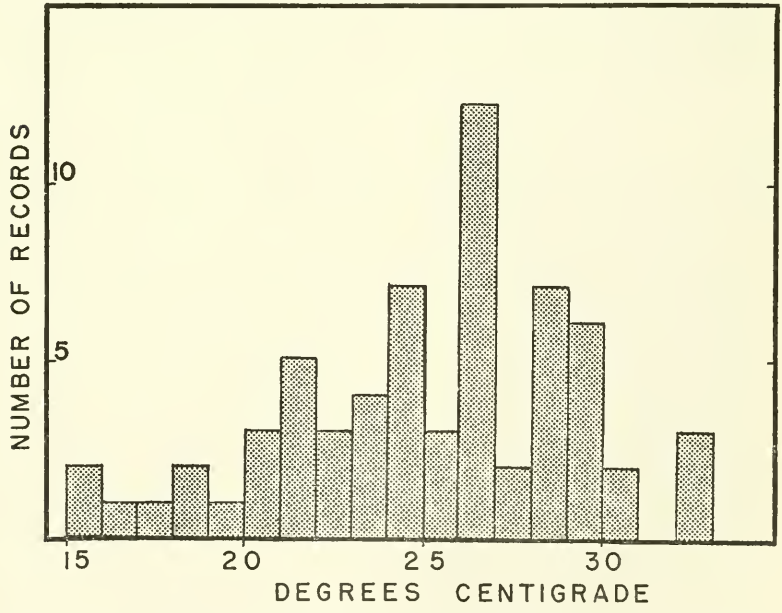


FIG. 7. Air temperatures recorded at captures of the racers whose records were used in Fig. 6. An active racer typically maintains, by basking, a bodily temperature several degrees warmer than the air.

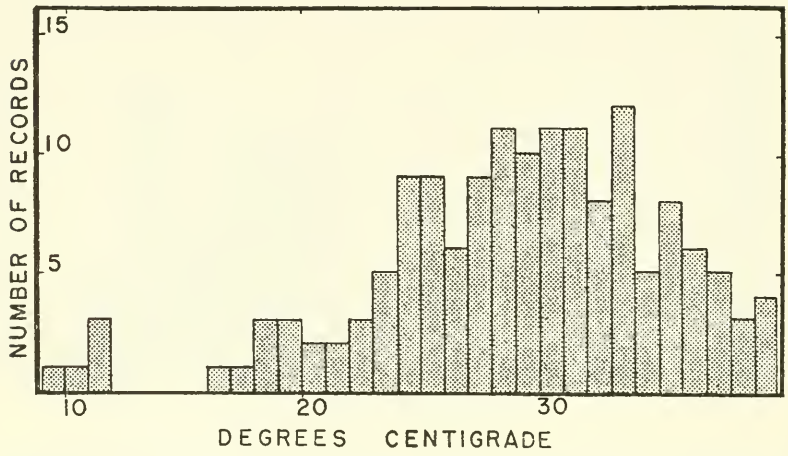


FIG. 8. Bodily temperatures of blue racers found in live-traps at Harvey County Park. Opportunity to regulate temperature by behavior was limited in these snakes in traps, which tended to match ambient temperatures.

in a spot strategically situated for catching grasshoppers. More than half her body was exposed to sunshine and air temperature was slightly above 34° Centigrade, yet the snake showed no sign of discomfort, and for the several minutes that she was kept under observation, did not attempt to withdraw into the shade.

At the Harvey County study area, bodily temperatures were recorded in many of the racers that were caught in traps. These records are much less significant than the records obtained from racers caught by hand and promptly checked for bodily temperatures. The temperatures of the trapped snakes may, to a large extent, reflect the temperatures of air and soil at the time. However, despite their confinement, the trapped racers probably were able to exercise some control over their temperatures by shifting from shade to sunshine, or from the top of the trap to its bottom, where they would be in contact with the substrate. In most of the racers removed from traps, as in those caught by hand, bodily temperatures were somewhat above air temperatures, but the difference was less in the former group of snakes. Figure 8 shows the bodily temperatures of these snakes removed from traps. Occasionally racers died in the traps from overheating. On July 2, 1960, each of two racers in traps had temperatures of 39.4°. One of these was especially vicious and frantic in its attempts to escape, but otherwise seemed unharmed. The second racer was dead, seemingly having succumbed just before it was found. Probably

prolonged exposure to temperature in excess of 39° would always result in death of the snake. Racers and other snakes that had become overheated in the traps and were nearing exhaustion had a characteristic limp feel when they were handled. In June, 1960, heat tolerance of a halfgrown racer was compared with that of several other snakes including a copperhead, garter snakes, and ringneck snakes. Each snake in turn was enclosed in a plastic tube plugged with cotton at one end, the snake having a quick-reading thermometer taped in place for a rectal reading. The tube was then placed in sunshine. Over periods of minutes the enclosed snake passed through a characteristic cycle. Soon it would begin to register discomfort as its temperature rose rapidly. Its struggles would become increasingly violent, then would cease abruptly. The snake would suddenly collapse, its body mostly limp, but knotted in slow contortions, its mouth gaping widely. Within a few seconds all movements would cease, but in each instance the seemingly dead snake was soon revived by holding it in cold running water. The copperhead, garter snakes, and ring-necked snakes all collapsed at temperatures near 41°. At this same temperature the racer showed signs of acute discomfort, but did not collapse even after many minutes of exposure. Probably more protracted exposure at this level would have been fatal to the racer as well as to the other kinds tested.

Home Range and Movements

Blue racers that were recorded on more than one occasion were rarely caught again at the original location. For different individuals, distances between capture points ranged from zero up to a little more than three-fourths of a mile. The area of concentrated study was a mile and a half in greatest diameter; there was scant opportunity for capturing racers that moved greater distances. Even those that moved as far as a mile would have passed beyond the boundaries of the study area in most instances. Many of the marked racers that disappeared from my records probably moved beyond the limits of the study area. Nevertheless, in the great majority of instances, the distances between successive capture points for the same individual were relatively short, indicating that each racer tends to remain permanently in a restricted area.

Most captures were made in the type of grassland or brush that provides favorable habitat for the racer during the season af activity, but many other captures were made in woodland along the rock

ledges where the snakes come to hibernate. Four different types of movement may be recognized: 1) those in the rock ledge area where hibernation occurs; 2) those between the area where the summer is spent and the hibernation ledge—an actual small scale seasonal migration which takes place in spring and autumn—3) those within a home range, which are part of the day-to-day activities of the racer, and, 4) wandering movements by which the racer shifts its activities, perhaps permanently, from one area to another. In the records of any one snake these different types of movements cannot always be sorted with certainty. Each type will be discussed separately.

Relatively few movements along the ledges were recorded. It seems that having migrated to a ledge, the racer promptly finds its hibernaculum and retires for the winter. In spring there is equally prompt scattering of the emerging racers, which no longer find the ledge attractive. Most recorded movements along the ledges were short. Of 76 movements, nine exceeded 1000 feet, and only four others exceeded 500 feet. Most of the shorter movements were recorded within an autumn season, but several were recorded after the lapse of one or more seasons of activity. The longer movements were as follows: 1250 feet after 8 seasons (male); 1300 feet after three seasons (female); 1600 feet after one season (female); 2000 feet after one season (female); 2280 feet after seven seasons (male); 2200 feet in same season (female); 2410, 2600, and 3200 feet, each after one season (all males). The trend of these records suggests that the tendency to return year after year to the same hibernaculum is not strong; after using one for a period of years, the racer may abandon the stretch of ledge and, starting out in the opposite direction from its summer range, find a new hibernaculum as much as half a mile from the old one. Records of distances between capture points on the ledges for individual racers are shown in Fig. 12.

A total of 124 movements between summer ranges and ledges were recorded, and the distances averaged 1309 feet—approximately a quarter mile. Some racers living in hilltop fields may have had home ranges that included rock ledges, or at least were adjacent to them. In such instances no seasonal migrations would have been necessary to reach hibernacula in the autumn and summer ranges in the spring. Several short movements—100 feet, 150 feet, and 200 feet—can be explained on the basis that home ranges and hibernation ledges overlapped or were near at hand, but most

of the movements were longer. The longest movement was 4020 feet, after a lapse of four seasons. Twenty-four movements exceeding 2000 feet were recorded. For these the intervals between captures averaged more than double the time for the remaining movements, indicating that the longtime permanent shifts were involved in many instances.

For all the racers living in bottomland, ranges were separated from ledges by areas of wooded hillsides averaging approximately 700 feet across. These relatively unfavorable areas had to be traversed in the course of the semi-annual migrations. Even some

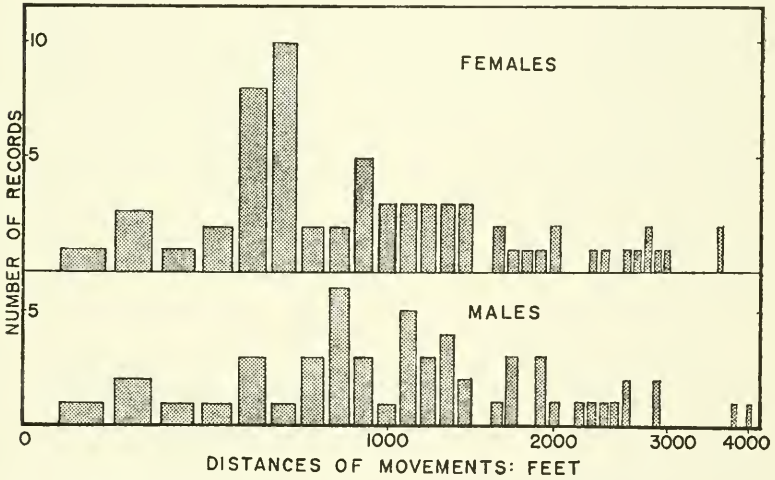


FIG. 9. Histogram of movements of blue racers between hilltop rock outcrops used for hibernation, and summer habitat on the Reservation and Rockefeller Tract. Movements of females tend to be somewhat shorter than those of males.

of the racers that lived in hilltop fields apparently crossed wooded slopes in order to reach distant hibernation ledges, or else each reached the ledge by a roundabout route although it could have found a ledge much nearer its summer range. For the 124 ledge-to-field and field-to-ledge movements, the median distance was 1030 feet. The sexes were almost equally represented in this sample but the average distance for the 55 males—1425 feet—notably exceeded that for the 69 females—1220 feet. These movements are shown in Fig. 9.

McCauley (1945:76) in Maryland described what seemed to be incipient territoriality in a large male racer that remained several hours in a small area, crawling about conspicuously with head

raised, seemingly on patrol. When an even larger male racer intruded, the first one aggressively drove him away, but neither paid any attention to a king snake that was also on the area. Other authors have noted the attachment of a racer to a small familiar area. Conant (1938:53) wrote that many of the racers he saw sought shelter in definite retreats. One of these racers was seen resting on top of a brush pile four times in a single afternoon, and each time it followed the same route to the same inaccessible spot beneath the brush.

My own observations do not bear out the idea that racers maintain regular territories, since several males may be present within a small area, even in the breeding season. Hostile behavior between males has not been observed by me under natural conditions, and in confinement has been seen only in instances of self defense. Like the racer Conant observed on a brush pile, individuals may linger in the vicinity of a favored shelter or foraging area for periods of hours, but such associations are ephemeral, and soon the snake moves on. In a uniformly favorable habitat a racer may cruise about freely in tall grass or brush. Individuals that I have attempted to follow, after flushing them or releasing them from traps, often covered distances of 100 to 300 feet within periods of a few minutes before I lost them. In such instances I maintained sufficient distance between myself and the snake so that the latter was not actively escaping. Probably the snake was not aware of pursuit in most instances, although I was able to glimpse it through the stems of grass, weeds, or shrubs, or was informed of its course by the swaying tops of grass and other vegetation.

For many of the racers captured over periods of years it was possible to plot "minimum home ranges" in the areas that they occupied. One caught 12 times in five consecutive years will serve as a typical example. There were seven locations involved; three captures were made at one point and two captures at each of two others; the other five locations were each represented by a single capture. One of the seven locations was for a capture made at a rock ledge in October, and hence can be eliminated from considerations of home range. The other six locations are based upon captures made from late May to early August, and they form a rhomboid pattern, with three locations in alignment on one side and two others inside the quadrangular figure formed by the five outlying points. Obviously such a group of records gives some idea of the location and extent of the snake's activities but the in-

formation is far from complete. As shown by Odum and Kuenzler (1955), a much larger series of records, usually several dozen, with eight or more marginal locations, is necessary to illustrate even an approximation of the actual home range. Under the conditions of my study such a series of records was unattainable. Few if any of the racers recaptured had more complete series of records than the one mentioned above.

For 20 racers the records were sufficiently numerous and well distributed to permit plotting of minimum home ranges. One of these ranges was hexagonal, nine were pentagonal, eight were rhomboidal and three were triangles. In four instances the area encompassed was broken by woodland, indicating that the home range comprised two or three disjunct segments. In all instances the smaller segments were triangular. The 20 minimum home ranges averaged 6.6 acres (3.2 to 12.8). The 15 ranges of males averaged 7.3 acres, whereas the five ranges of females averaged only 4.5 acres, but the sample is too small to be relied upon for differences in the sexes.

In an earlier publication (Fitch, 1958:73) I discussed an alternative method for determining size of home range in animals that

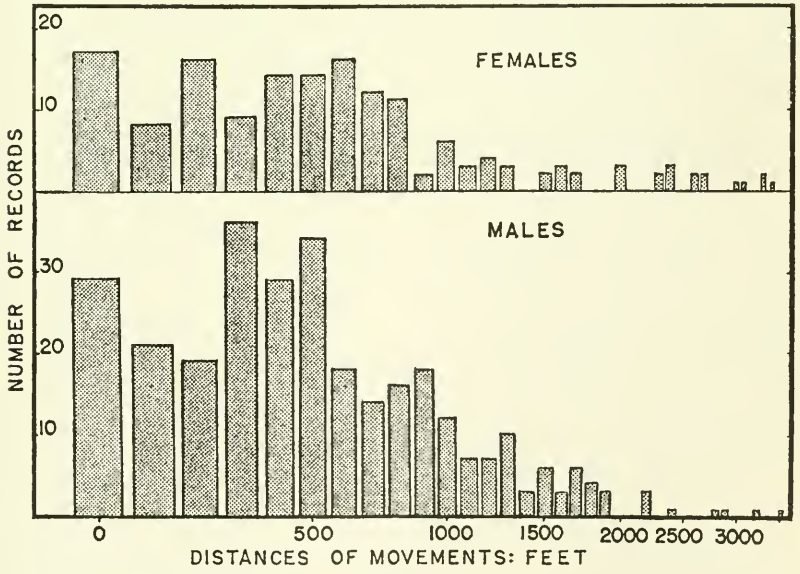


FIG. 10. Movements of blue racers within or between areas of summer habitat on the Reservation and Rockefeller Tract. The trends are much alike for males and females.

move about freely within a chosen area, not having their movements restricted by attachment to a specific home base. Ordinarily any two records of the animal within its home range will be separated *on the average* by a distance equal to half the diameter of the area. Assuming that home ranges in general tend to have a circular shape, except as restricted by limiting environmental factors, the area can be easily computed from the average recorded movement—the home range radius. It is necessary, of course, to have a sufficiently large number of records of movements to obtain an average that is statistically reliable.

A major problem is that of recognizing movements that involve an extension of the original range or a shift away from it to a new area. A few exceptionally long movements were recorded. If these are included in the computations of home range, they greatly increase the average distance, probably introducing error. Also, the number of exceptionally short movements was greater than might have been expected if all locations of capture are at random to each other. In some instances a racer newly released may have blundered into the same trap again, or into the trap at the opposite end of its drift fence. In other instances traps may have been so strategically situated with respect to preferred travel routes that they caught the same snakes repeatedly. In still other instances, the range of an individual might have been mostly outside the study area, with only one end or corner overlapping the trap sites.

A total of 471 records for consecutive captures in field areas is available, 305 for males and 166 for females. In 20 instances successive sites of capture were the same and movement was recorded as zero. Of the 471 records, 207 involved a relatively long time span, including at least one hibernation period; the remaining 264 were based upon successive records within the same season of activity. The trends were much the same in the records involving a longer time span (up to four years) as in those records involving captures made in a single season, but for the longer periods there were some exceptionally long movements, and relatively few short movements of less than 100 feet.

Records of male racers and those of females were used for separate computations. For each series, the ten per cent of movements that were longest and the ten per cent that were shortest were eliminated from consideration in calculation of the average distance between points of capture. For the remaining 244 records of males an average movement of 595 feet was calculated, and for

132 records of females an average movement of 574 feet. These distances, if accepted as typical home range radii, would represent home ranges of 26.3 acres for males and 23.8 for females. In an earlier discussion of spatial relationships in the racer (Fitch, 1958: 119), based upon relatively scanty data, I estimated the home range to be approximately 23 acres in males. But with only nine records for female racers I calculated the home range to be 9.7 acres.

The disparate figures obtained from plotting minimum home range and from calculating average home range radius are not irreconcilable, since a minimum home range based on only four or five points would ordinarily include only a fraction of the actual range. Distances up to 1500 feet are included in the calculation of home range. It seems that home ranges often have a diameter of this magnitude or a little larger, although the estimated average diameter is 1140 feet. Home ranges probably most often deviate from circular shape to form an ellipse, with one diameter markedly exceeding the other. Woodland, water, roads, buildings, or cultivated fields, or other areas that are unfavorable or uninhabitable often form the boundary of a home range and influence its shape.

Many of the longer movements constituted clear-cut shifts in range. In one exceptional instance a large adult female captured in the northeastern part of the Reservation on June 22, 1950, was released 21 days later at a point 3900 feet southwest of the place of capture. On May 27, 1960 she was caught within 600 feet of the original location, seemingly having made a homing movement. Among the nine racers recorded to have made longest movements (exclusive of those movements made to or from hibernacula) four were recorded also to have made later long movements in the reverse direction, probably returning, each to its original home range, although in every instance the return movement was somewhat less than the original. A female of two-year-old size when first captured on September 2, 1957, was recaptured 3100 feet southeast on May 10, 1958. On August 7, 1959, she was recaptured again 2400 feet from the second location in the direction of the original capture. Similarly, in a three-year-old female a shift of 2730 feet was recorded at the second capture after 21 months, and at the third capture 14 months after the second, a return trip of 2360 feet had been made. A second-year female made a trip of 2640 feet between May 17 and October 1, 1960; by May 1961 she had returned 2000 feet to the vicinity of her original capture. From one year to the next an adult male shifted 2450 feet; after another year he had

moved back 1550 feet. Most of the longer movements recorded were those between home ranges in fields and hibernacula along ledges, but in this class of movements, distance was somewhat proportional to elapsed time. For 59 such movements exceeding 2000 feet the average was 3.1 years, whereas for 114 field-to-ledge movements of less than 2000 feet, average elapsed time was 1.6 years. This trend suggests that over periods of years a racer is likely to shift its range or its hibernaculum or both.

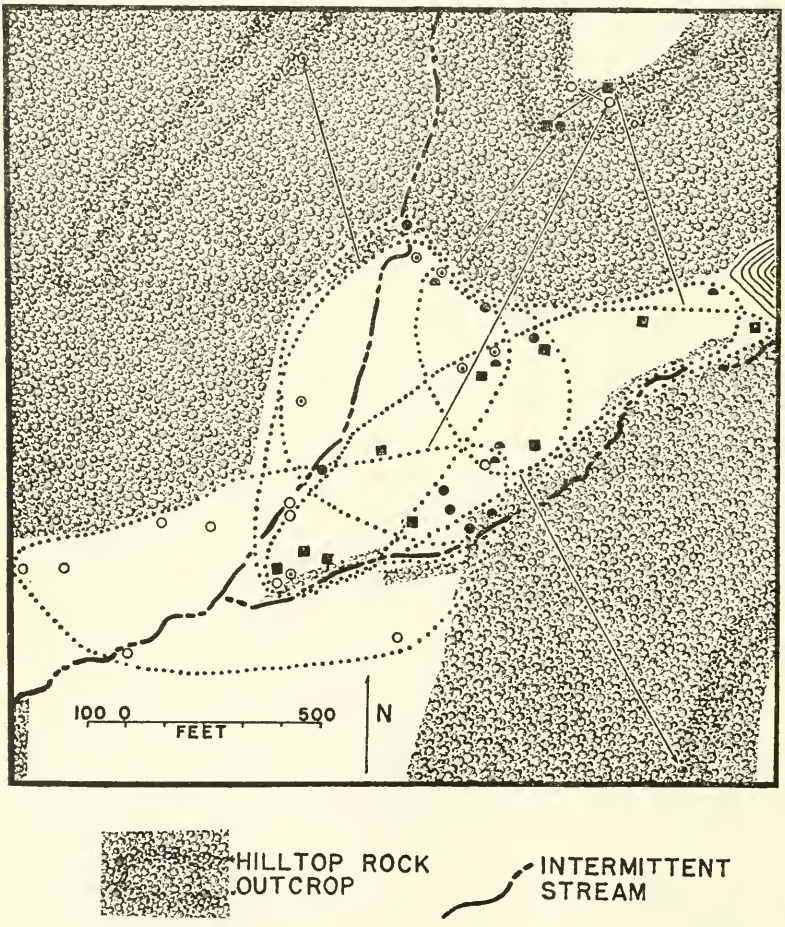


FIG. 11. Map showing home ranges of five blue racers, as indicated by numerous captures in successive summers, in small valley where Reservation headquarters are located, and spatial relations of their hibernacula, as represented by points of capture along hilltop limestone outcrops. In spring and autumn, traveling to and from hibernacula, the snakes migrate across wooded slopes. Each "minimum home range" is enclosed in a dotted line, and a distinctive symbol is used to show successive points of capture for each snake.

Average elapsed time between captures was 7.7 months. In the 471 field-to-field movements recorded, 53—slightly more than eleven per cent—exceeded 1500 feet and can reasonably be considered shifts of home range. The average elapsed time between captures for this group of snakes was 9.5 months. The evidence suggests

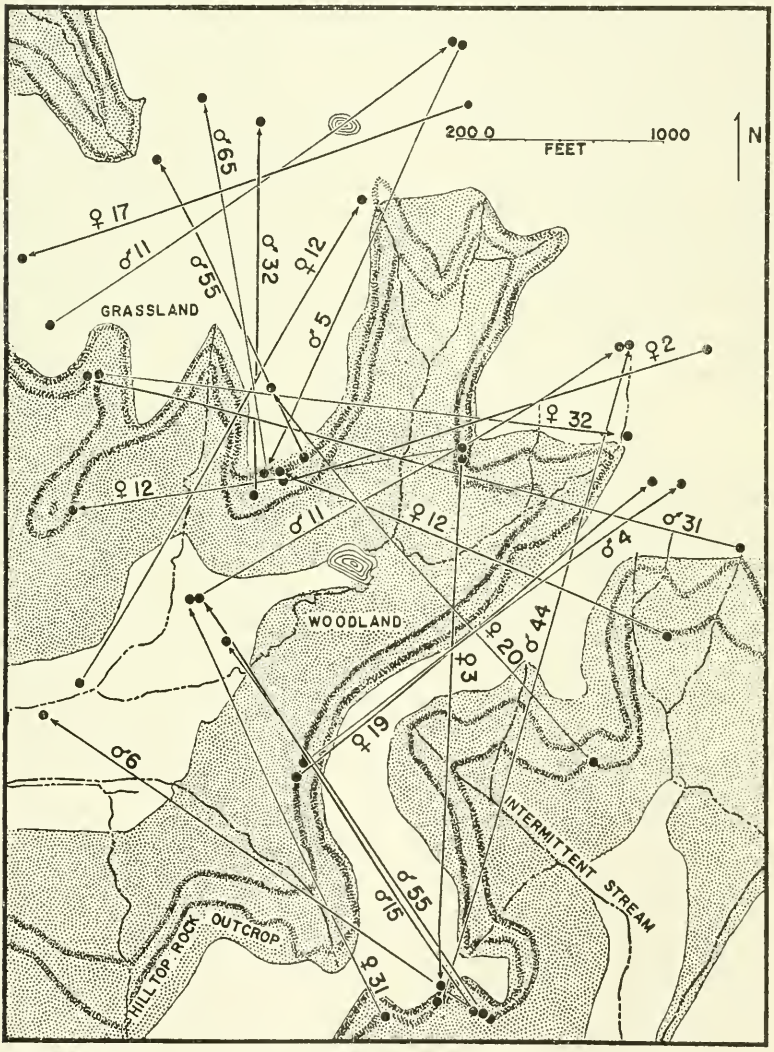


FIG. 12. Map of 600-acre area of Reservation and Rockefeller Tract, including parts where field study was most concentrated, showing movements of the 20 blue racers recorded to have shifted over the longest distances. The figure following the sex sign of each individual indicates number of months elapsed between the captures at the localities represented by the dots.

that, even in an area of favorable habitat, somewhat more than ten per cent of the racers in a population annually shift their home ranges somewhat, but that many stay in the same home range for periods of years or perhaps throughout life.

Shifts in range were especially noticeable where availability of suitable habitat underwent seasonal change. Along the north edge of the Reservation, prairie adjoined cultivated fields where grain or hay was grown. Until late May, the cultivated crops made little growth and the fields were almost bare. They provided insufficient shelter for the racers, which tended to keep to the prairie, where old grass of the previous year's growth furnished them with ample cover. Later in the season, crops of oats, wheat, and alfalfa constituted suitable cover for the racers, and many of them shifted their ranges to the cultivated fields, but corn and milo crops were much less adequate for their needs. After harvesting of crops, cover in the fields was again inadequate for the racers' needs, and they tended to retreat to edge situations, or to adjacent prairie.

Food Habits

Methods of Obtaining Prey

The racer hunts by stealth, but actively, obtaining its prey by keen eyesight and swift movements. Wright and Bishop (1915: 160) wrote that because of its great speed it can catch anything that moves on the ground. As a racer moves stealthily through dense vegetation, its dull, uniform dorsal color blends well with the surface litter of dead plant material. In prowling, the snake glides along rapidly and alertly, in a jerky fashion, with frequent momentary pauses and changes of direction. Because of its inconspicuousness, it is not likely to be detected by the prey until it is close at hand. The snake is ready to dash in pursuit of any small animal that flies, jumps or runs to escape.

On August 27, 1955, my daughter observed a large racer hunting among tall weeds at the edge of the pond on the Reservation. Several times in the course of its movements, it flushed small frogs (*Rana pipiens*) and each time the snake darted in unsuccessful pursuit of the rapidly hopping frog. On several occasions I have been led to a blue racer by the distressed croaking of a frog that the snake had captured. In each instance, despite my cautious approach, the racer saw me before I detected it, and then darted away, abandoning its prey. On one occasion, while I was still a few yards from the racer, and before the latter had detected me, the

frog broke free and hopped away rapidly through tall grass and weeds, and after several leaps, hid, concealed by dense screening vegetation. The racer darted in pursuit but could not find the frog. For several minutes the snake persisted in an active search; with forebody elevated and head held high, it would turn first in one direction and then in another, with nervous, jerky movements, obviously keyed up to a high pitch of excitement. Then it became aware of my presence, lowered its head, and glided away rapidly, abandoning the search.

Although the racer depends to a large extent on sight to find its prey, scent may play some part also, as indicated by the presence in the food of young mammals taken from nests, some probably found underground. Near Garnett, Kansas, on May 4, 1952, Richard B. Loomis found a racer attacking a collared lizard (*Crotaphytus collaris*) beneath a large flat rock. The lizard was retaliating by biting the snake's neck. The posterior part of the snake protruded into the open, and its thrashing had directed the attention of the observer to it. Whether the racer first found the lizard under the rock, or followed it there after flushing it in the open is unknown.

An encounter between a large blue racer and an adult Great Plains skink (*Eumeces obsoletus*) on August 30, 1948, was described as follows: "The skink, grasped by one flank, had twisted back and seized the skin of the snake's neck in a bulldog grip, and they lay interlocked, motionless except for their rapid panting, and occasional straining of the skink to bite harder or of the snake to shift its grip and work its jaws toward the skink's head. The racer broke the skink's grip, and began to swallow it head first. When only the hind legs and tail of the skink still protruded from the racer's mouth, I lunged forward in an attempt to catch both reptiles. With a sudden movement the snake disgorged the skink, which darted away into the grass and escaped" (Fitch, 1955:78).

Composition of Food

Many authors have contributed to knowledge of the racer's food habits. In most instances the records have been few or casual, but several intensive studies have been made, notably by Surface (1906) in Pennsylvania, Ortenburger (1928) for the species as a whole, Uhler, Cottam and Clark (1939) in Virginia, Clark (1949) in Louisiana, Auffenberg (1949) in southern Texas, Hamilton and Pollack (1956) in Georgia, and Klimstra (1959) in southern

Illinois. However, the findings of different authors are not strictly comparable; some have made general statements concerning the food habits but have mentioned specific items only when these were considered unusual. Certain authors have listed individual prey animals eaten; others have indicated the percentages (in bulk or in frequency) that the different kinds of prey comprised. Some writers have identified food animals only in broad categories such as "insect," "beetle" or "snake" while others have undertaken specific determinations for all the prey or for certain taxonomic groupings that were subjects of special interest.

For the eastern black racer (*C. c. constrictor*) the following food items have been recorded: 1 robin (*Turdus migratorius*, Storer, 1839:226); 1 copperhead (*Agkistrodon contortrix*, Verrill, 1869:158); 1 weasel (*Mustela* sp.—presumably the diminutive *M. rixosa*—Atkinson, 1901:148); 3 undetermined mammals, 1 rabbit, 1 undetermined mouse, 7 voles (2 *Microtus* sp., 4 *M. pennsylvanicus*, 1 *Clethrionomys gapperi*), 1 undetermined bird, 2 robin eggs, 2 garter snakes (*Thamnophis sirtalis*), 1 water snake (*Natrix sipedon*), 1 grass snake (*Opheodrys vernalis*), 1 green frog (*Rana clamitans*), 1 wood frog (*R. sylvatica*), 1 grasshopper (*Melanoplus femur-rubrum*) 2 camel crickets (*Ceuthophilus* sp.), 5 moths (cecropia, regal, imperial), 4 beetles, 1 currant worm, 1 ichneumonid wasp (*Nematus ribesii*), 1 currant worm (Surface, 1906: 170); 1 ribbon snake (*Thamnophis sauritus*, Ditmars, 1907:282); 3 snakes (1 *Liopeltis vernalis*, 1 *Storeria occipitomaculata*, 1 undetermined), 6 white-footed mice (1 *Peromyscus leucopus*, 5 *P. nuttalli*), 1 vole (*Microtus pennsylvanicus*), 16 crickets (9 *Gryllus pennsylvanicus*, 4 *G. assimilis*, 2 *Miogryllus verticalis*, 1 *Nemobius fasciatus*), 2 grasshoppers (*Dissosteira* sp.), 1 lepidopteran, 3 elaterid beetles (Ortenburger, 1928:200). Richmond and Goin (1938:310) recorded finding the stomach of a black racer crammed with June beetles (*Phyllophaga*). Conant (1938:53) recorded a black racer from Ohio that had a smaller individual of its own species in its stomach. The smaller snake contained a caterpillar. Uhler, Cottam and Clark (1939:34) found food in 16 of 34 black racers from Virginia. Mammals, including a shrew (*Blarina brevicauda*), a mole, a flying squirrel (*Glaucomys volans*), a microtine, and a mouse (*Peromyscus* sp.) made up 26 per cent, 2 worm snakes (*Carphophis amoenus*), 2 ring-necked snakes (*Diadophis punctatus*), and 1 water snake (*Natrix sipedon*) made up 25.6 per cent, 5 birds including a warbler and a sparrow, made up 17.75 per cent; 2 frogs (*Rana* sp.) made up 9.38 per cent, 1 fence lizard (*Sceloporus undulatus*) made up 6.25 per cent, and insects, including cicadas (*Tibicen* sp.) and larval lepidopterans, made up 15.09 per cent. In Indiana, Minton (1944:457) examined 11 food-containing stomachs; there were rodents in six, snakes in five, a tree frog in one, and insects (cicadas, large grasshoppers) in four, and another black racer was found swallowing a small box turtle (*Terrapene carolina*). In Maryland, McCauley (1945:75) examined eight digestive tracts and recorded a shrew (*Blarina brevicauda*) in one, an unidentified mammal in one, 2 small cicadas in one, 2 small chickens in one, a fence lizard (*Sceloporus undulatus*) in one, and frogs and toads (including *Hyla crucifer*) in one; a ninth snake had eaten a half grown rat. In Connecticut, Finneran (1948:124) observed a large black racer eating a 21-inch garter snake (*Thamnophis sirtalis*). Duellman (1951:338) recorded a black racer in Greene County, Ohio, swallowing a large garter snake (*Thamnophis sirtalis*). In Kentucky, Barbour (1950: 104) recorded remains of an unidentified snake in one stomach.

Many authors likewise have recorded food of the southern black racer (*C. c. priapus*). In Georgia, Wright and Bishop (1915:160) recorded finding 2 racerunners (*Cnemidophorus sexlineatus*), a skink (*Lygosoma laterale*), 4 green tree frogs (*Hyla cinerea*) and 1 pine woods tree frog (*H. femoralis*) in

stomachs. They also stated that the toad (*Bufo lentiginosus* [= *terrestris*]) was the most important article of food. Burt and Hoyle (1934:205) wrote that a racer from Rogers County, Oklahoma, had eaten an adult male collared lizard (*Crotaphytus collaris*). In Florida, Carr (1950:80) found one of these black racers eating a leopard frog (*Rana pipiens*). Hamilton and Pollack (1956:523) examined digestive tracts of 62 and found food in 57, comprising the following percentages by volume: *Lygosoma laterale,* 34.2; *Eumeces fasciatus* and *E. egregius,* 11.3; *Cnemidophorus sexlineatus,* 8.8; *Sceloporus undulatus,* 3.5; undetermined lizard, 3.5; *Opheodrys aestivus,* 6.6; *Diadophis punctatus,* 3.1; *Storeria dekayi,* 1.6; *Coluber constrictor,* 1.8; *Heterodon platyrhinos,* 1.8; *Masticophis flagellum,* 1.8; *Rana* sp., 5.3; *Hyla cinerea,* 1.8; *Hyla versicolor,* 1.8; *Peromyscus,* 1.8; undetermined rodent, 1.8; lepidopterous larva, 1.7.

In southern Illinois in an intergrading population of racers intermediate between *C. c. priapus* and *C. c. flaviventris,* Cagle (1942:188) examined several stomachs and found 1 chipmunk (*Tamias striatus*), 2 voles (*Microtus* sp.), 2 mice (*Peromyscus* sp.), 2 green snakes (*Opheodrys* sp.), 1 water snake (*Natrix sipedon*) and grasshoppers. From this same population Klimstra (1959:212) examined 137 digestive tracts of which 115 contained food as follows: 194 locustids, 118 gryllids, 17 undetermined beetles, 13 carabids, 6 scarabaeids, 10 lepidopterans, 9 hemipterans, 1 hymenopteran, 2 homopterans, 1 dipteran, 17 undetermined insects, 73 *Peromyscus* sp., 19 *Microtus ochrogaster,* 9 *M. pinetorum,* 12 *Sylvilagus floridanus,* 3 *Scalopus aquaticus,* 3 *Rattus norvegicus,* 4 *Mus musculus,* 2 *Tamias striatus,* 2 *Synaptomys cooperi,* 16 *Rana pipiens,* 8 *Acris crepitans,* 2 *Rana clamitans,* 2 *R. palustris,* 1 *R. catesbeiana,* 4 *Hyla crucifer,* 3 *Pseudacris nigrita,* 4 *Lampropeltis calligaster,* 4 *Sceloporus undulatus,* 4 *Chrysemys picta,* 1 *Heterodon platyrhinos,* 1 unidentified reptile, 4 *Sturnella magna,* 1 *Otocoris alpestris,* 4 unidentified birds. Percentages by volume of the various categories in this sample were: insects, 39.1; mammals, 32.9; amphibians, 10.8; reptiles, 8.3; birds, 6.3; miscellaneous, 2.6.

Food of the "buttermilk snake" (*C. c. anthicus*) is known only through Clark's study (1949:249). In an unstated number of examinations he found "mice" in 25, "rats" in five, lizards (*Sceloporus undulatus* and perhaps others) in eight, frogs (*Rana pipiens*) in seven, and birds in three.

The food of *C. c. stejnegerianus* is known only from the work of Auffenberg (1949) but his sample was based on 206 racers that had food, among the total of 291 recorded. Unfortunately, he did not present actual numbers of the various prey animals, but divided the food into seven categories and listed these as percentages. He did not indicate whether the percentages represented volumes or numbers of individual occurrences, and evidently there was some error in computation since his combined percentages totalled 111. The categories and their percentages were as follows: grasshoppers, 42.5; crickets, 13.5; miscellaneous insects, .6; earless lizards (*Holbrookia* sp.), 40.1; scaly lizards (*Sceloporus* sp.) 2.1; frogs (*Rana* sp.) 10.0; rodents, 2.2. Auffenberg divided his sample of racers into five size classes, and showed that the smaller snakes fed chiefly on insects whereas vertebrates were increasingly prominent in the food of the larger snakes.

The food of *C. c. mormon* is known chiefly through the work of Ortenburger (1928:228) who cited instances of a skink (*Eumeces skiltonianus*) and a young garter snake (*Thamnophis sirtalis*) being eaten, and listed the following items from 24 stomachs that he examined: 7 decticids, 8 acridids, 5 oedipines, 1 tryxaline, 6 *Melanoplus* sp., 3 *M. mexicanus,* 2 *M. devastator,* 1 *M. bivittatus,* 2 *Dissosteira carolina,* 1 *Chortophaga viridis,* 3 *Neduba carinata,* 3 *Trimerotropus* sp., 7 *Hippiscus* sp., 2 *Steiroxys* sp., 3 *Canoula pellucida,* 2 *Stenopelmatus fuscus,* 2 *S. pictus,* 4 *Gryllus assimilis,* 4 *Ceuthophilus* sp., 1 *Pristoceuthophilus pacificus,* 6 *Gammarotettix bilobatus* and 2 cicada nymphs. Grinnell, Dixon and Linsdale (1930:149) found that one of these racers had eaten a cricket. Fitch (1936:644) found another in the act of swallowing an adult vole (*Microtus californicus*), and recorded (1935:18) that two alligator lizards (*Gerrhonotus multicarinatus*) were found in the stomach of still another.

Woodbury (1931:75) recorded that a racer from Utah had a sagebrush scaly lizard (*Sceloporus graciosus*) in its stomach. Of the specimens examined in the University of California Museum of Vertebrate Zoology, no. 17256 from the Mad River, Trinity County, California, had eaten an alligator lizard (*Gerrhonotus coeruleus*), and no. 10120 from Yolla Bolly Mountain in the same county had eaten a bird (unidentified) and a Jerusalem cricket (*Stenopelmatus* sp.).

Several authors have published specific information regarding the food of *C. c. flaviventris*. Hurter (1911:171) caught a blue racer in the act of swallowing a copperhead (*Agkistrodon contortrix*). Taylor (1892:331) recorded finding garter snakes in several large racers. Pope and Dickinson (1928:53) recorded instances of blue racers feeding on racerunners (*Cnemidophorus sexlineatus*). Ortenburger (1928:181) examined 22 stomachs and recorded: 1 large garter snake (*Thamnophis sirtalis*), 1 vole (*Microtus pennsylvanicus*), 1 frog (*Rana* sp.) 31 crickets (*Gryllus assimilis*), 4 decticines, 2 acridids, grasshoppers (1 *Hippiscus*, 2 *Melanoplus* sp., 1 *M. confusus*, 1 *M. differentialis*, 1 *Dissosteira carolina*, 1 *Sphargemon collare*, 1 *Trimerotropus* sp., 1 *Orphulella* sp., 1 *Chloealtis conspersa*, 1 *Chortophaga viridifasciata*, 1 *Omaseus* sp., 1 *Pedocetes* sp.), and 2 caterpillars (1 noctuid, 1 sphingid). Gloyd (1928:123) recorded a hatchling glass lizard (*Ophisaurus attenuatus*) in the stomach of a juvenal racer. Force (1930:31) found a racer eating eggs from the nest of a cardinal (*Richmondena cardinalis*) and another racer eating eggs of a redwing (*Agelaius phoeniceus*). Gloyd (1932:403) recorded an observation of a racer overpowering and swallowing a copperhead. Anderson (1942:210) recorded remains of crickets and grasshoppers in feces. Hudson (1942:55) recorded a racerunner (*Cnemidophorus sexlineatus*) in the stomach of a juvenile and recorded an earless lizard (*Holbrookia maculata*) 3 lizard eggs, and 14 grasshoppers (*Melanoplus differentialis* and others) in the stomach of another. Marr (1944:484) found a harvest mouse (*Reithrodontomys montanus*) in one. Breckenridge (1944:118) recorded stomach contents including a garter snake (*Thamnophis sirtalis*), a frog (*Rana pipiens*), 3 crickets and 2 moths. Mossimann and Rabb (1952:27) recorded that a racer disgorged several grasshoppers. Fouquette and Lindsay (1955:411) recorded that a blue racer had eaten a harvest mouse (*Reithrodontomys* sp.). Carpenter (1958:114) recorded that one blue racer had eaten a green snake (*Opheodrys aestivus*) and another had eaten a grasshopper and a camel cricket.

Even though the sets of data cited above are not entirely comparable, certain trends are evident. The black racers of the eastern states (especially *C. c. constrictor* of more northern regions) take a high proportion of vertebrates in their prey. Among these vertebrates snakes especially are well represented and the black snake would seem to be of some importance as an ophiphagous predator. The birds and mammals taken include some that are bulky (robin, cottontail, and even a weasel—the most formidable prey eaten). Presumably the rabbits that were eaten were young. In samples from the eastern United States insects made up small to insignificant parts of the food; they were lacking entirely or at least were not mentioned in the samples examined by McCauley and Wright and Bishop. In the blue racer of the central states, insects (mostly grasshoppers and crickets) are much more prominent in the food and vertebrates correspondingly less prominent. The vertebrates eaten are largely lizards, small snakes and mice. *C. c. stejnegerianus* is much like *flaviventris* in the trend of its feeding. *C. c. mormon*

is less known than these subspecies in its feeding, but indications are that it takes a higher proportion of orthopteran insects and smaller proportions of mammals and snakes than do any of the other subspecies.

In my own field study a total of 1357 food records were accumulated, one of the largest samples known for any kind of snake. Most of these records were from the small area where my population study was carried on, and studies of other kinds of animals, including those that were the racer's prey, were simultaneously in progress. Because large collections of reference materials were available, it was possible to identify to species many of the prey items found, even though they were incomplete and highly fragmented because most of them were recovered from fecal material.

The prey is, of course, swallowed entire, and the recently swallowed items squeezed from the stomachs provide the best material for the study of food habits. However, relatively few racers had detectable food items in their stomachs; digestion is rapid and often the snake was in a trap for a day or more before it was found. Therefore the greater number of records were obtained from scats. The residue in scats consisted entirely of hard and indigestible parts such as the chitin of insects' exoskeletons and the hair, feathers, scales, teeth and occasional bone fragments of the vertebrate prey. The insects eaten could usually be counted individually by sorting parts, such as heads or hind legs. With mammals, birds and reptiles the hair, feathers, or scales did not permit counting of individuals—each occurrence was assumed to represent one individual but in some instances two or more may have been present. Amphibians, lacking indigestible dermal structures were in most instances not represented at all in the scats, since their tissues were more or less completely dissolved by the digestion of the snakes. Soft-bodied larvae of insects and other invertebrates conceivably could be likewise completely digested, but such occurrences must be rare, as most of the invertebrates known to be eaten have the mouth parts, at least, heavily chitinized.

Admittedly the factors discussed above would cause some bias in the percentage composition of the food determined from scats, but I believe that the amount of error introduced was slight, because, judging from the records of items from stomachs, amphibians are not eaten frequently, and even mammals are not eaten frequently enough so that there is much chance of a snake taking two or more individuals at the same meal, unless it is robbing a nest containing a litter of young.

The largest sample, based on 1008 food items, was obtained from 479 scats collected from the Reservation and Rockefeller Tract over the period 1949 through 1961. Items recorded were: 183 gryllid crickets (144 *Gryllus assimilis,* 36 *Gryllus* sp., 3 unspecified); 353 locustid grasshoppers (41 unspecified, 73 *Arphia simplex,* 67 *Melanoplus femur-rubrum,* 66 *M. bivittatus,* 39 *M. differentialis,* 17 *Melanoplus* sp., 15 *Dissosteira carolina,* 8 *Chortophaga viridifasciata,* 6 *Syrbula admirabilis,* 6 *Sphargemon equale,* 2 *Melanoplus scudderi,* 2 *Schistocerca obscura,* 1 *S. americana;* 94 camel crickets (*Ceuthophilus* sp.), 93 katydids (36 *Neoconocephalus robustus,* 15 *Orchelimum vulgare,* 15 *O. nigripes,* 6 *Conocephalus* sp., 4 *Orchelimum* sp., 2 *Amblycorypha inasteca,* 1 *Neoconocephalus* sp., 1 *Daihinia brevipes*); 7 cicadas (5 *Tibicen* sp., 1 *T. pruinosa,* 1 *T.*

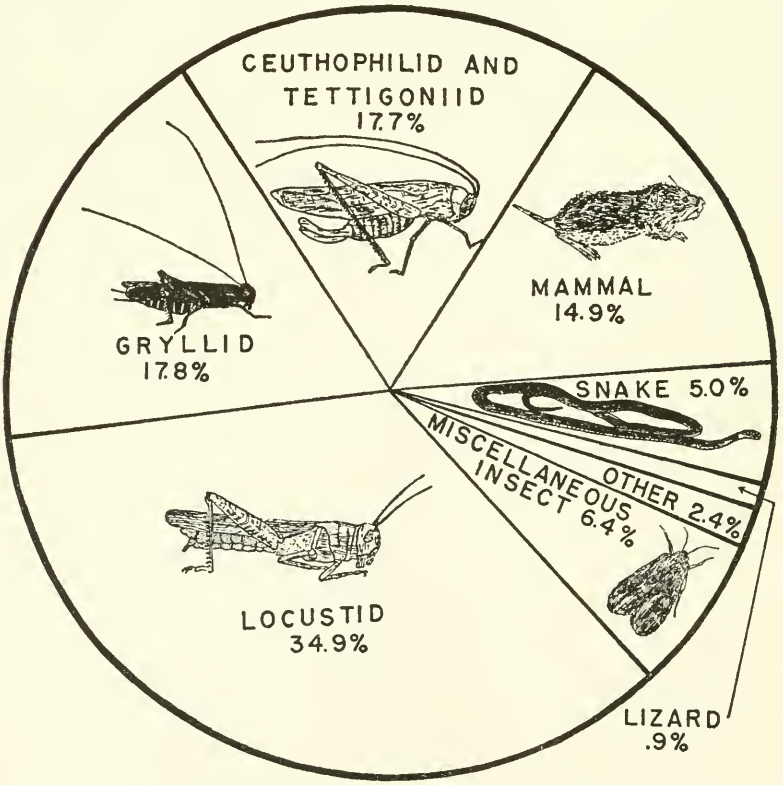


FIG. 13. Diagram showing percentage frequency of occurrence of various categories of prey in a sample of 1008 food items identified from scats and stomachs of blue racers from the Reservation and Rockefeller Tract. Insects, especially, orthopterans, made up the great majority of prey items taken.

lyrica); 45 unidentified insects; 17 beetles (including 1 *Phyllophaga*, 1 *Calosoma scrutator*, and 2 other carabids); 2 noctuid moths (*Mocis latipes*) and 1 caterpillar; 2 homopterans, 1 bee, 1 ant, 1 spider; 69 voles (59 *Microtus ochrogaster*, 9 *Microtus* sp., 1 *M. pinetorum*); 31 white-footed mice (15 *Peromyscus leucopus*, 14 *Peromyscus* sp., 1 *P. maniculatus*); 36 miscellaneous small mammals (6 *Cryptotis parva*, 4 *Sigmodon hispidus*, 4 *Reithrodontomys megalotis*, 3 *Blarina brevicauda*, 2 each of *Scalopus aquaticus*, *Sylvilagus floridanus*, and 1 unspecified shrew); 50 snakes (16 *Coluber constrictor*, 15 *Diadophis punctatus*, 14 *Thamnophis sirtalis*, 4 *Elaphe obsoleta*, 1 *Natrix sipedon*); 7 lizards (5 *Eumeces fasciatus*, 1 *E.*

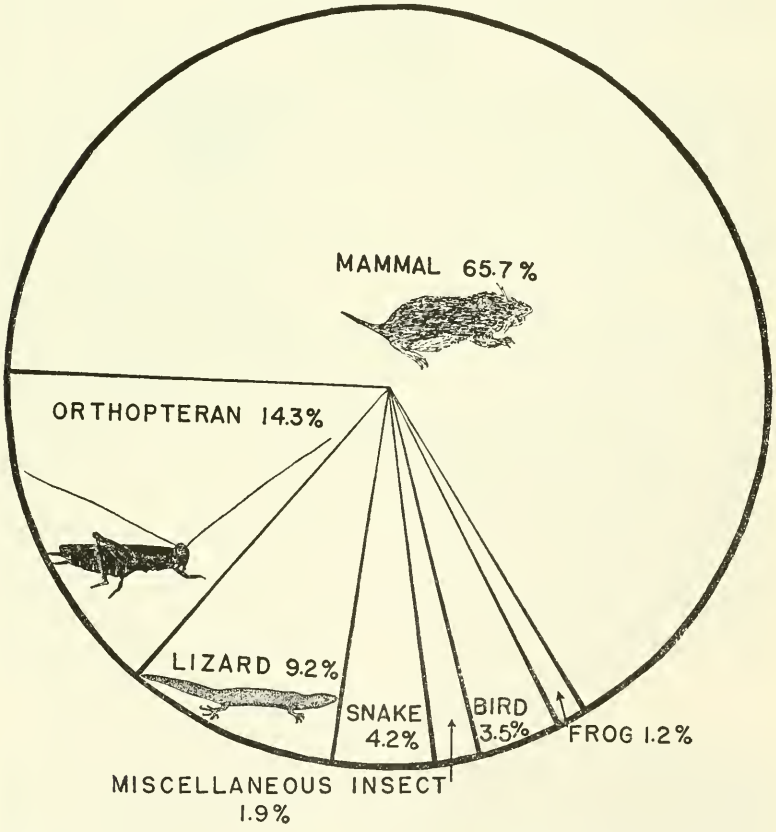


FIG. 14. Diagram showing estimated percentage by weight of various categories of prey in a sample of 1351 items, including all those represented in Fig. 13 and others from various parts of Kansas. Since the vertebrate items are on the average much bulkier than the insects eaten, vertebrates comprise most of the food, even though insects are eaten in much larger numbers.

obsoletus, 1 *Cnemidophorus sexlineatus*); 3 unspecified "reptiles"; 5 birds (none identified to genus); 3 bird eggs, 1 narrow-mouthed toad (*Gastrophryne olivacea*).

Over the same period that the sample of scats was collected, a much smaller food sample of 73 prey items was collected by squeezing recently eaten food from the racers' stomachs, or by finding the snakes actually swallowing their prey. These items from stomachs are listed separately because they include relatively more vertebrates than do the items from scats. A grasshopper or cricket eaten by a large racer might have passed undetected, while a relatively

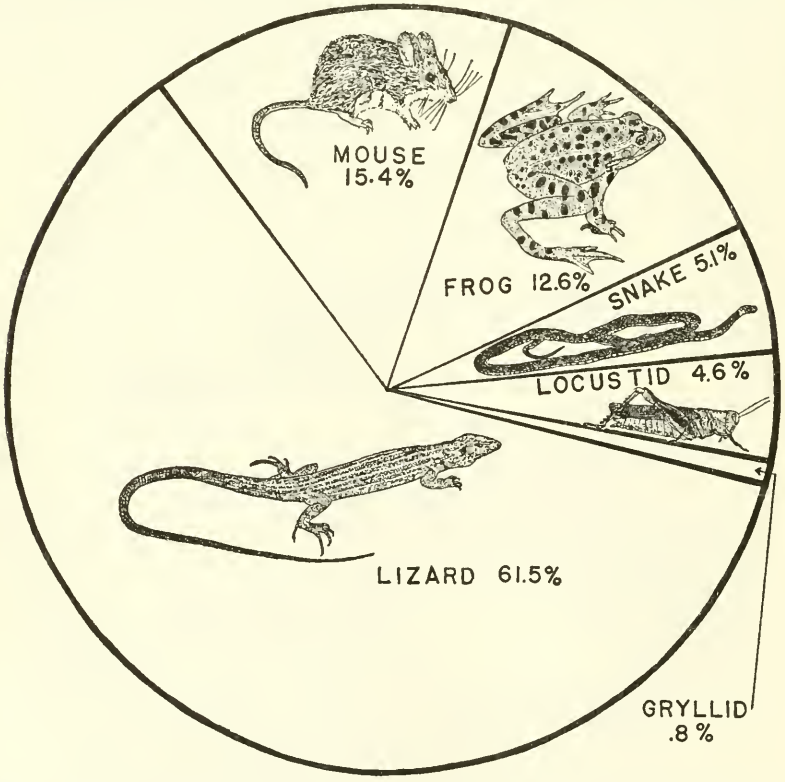


FIG. 15. Diagram showing estimated percentages by weight of various categories of prey in a sample of 69 food items squeezed out of stomachs of the blue racers captured at Harvey County Park. Most of the items were vertebrates, and lizards (*Cnemidophorus*) were especially prominent in the food at this locality. Samples of prey from scats (included in Figs. 13 and 14) and from stomachs show somewhat different trends, and neither is entirely representative of the actual feeding. Also, local differences in food sources are important.

large item such as a vole or lizard would have produced a conspicuous bulge in the snake that ate it, and would have excited the curiosity of the investigator. A second difference is that the items from stomachs included several frogs, whereas amphibians were absent from the much larger sample from scats. A third difference is that the many insects found in stomachs were all orthopterans with the exceptions of three noctuid moths and the larva of a moth. Miscellaneous insects, such as beetles, bees and ants recorded from scats were not found in stomachs. Amphibians eaten are digested so completely that no recognizable parts of them are to be found in scats, but remains of the insects previously eaten by amphibians are to be seen in racers' scats. If not recognized as secondary items, such remains might lead to erroneous conclusions regarding the racer's food.

The items from stomachs were as follows: 21 grasshoppers (5 oedipines, 4 tryxalines, 5 *Melanoplus bivittatus*, 3 *M. differentialis*, 1 *M. femur-rubrum* and one each of *Chortophaga viridifasciata*, *Dissosteira carolina*, and *Sphargemon equale*); 8 crickets (*Gryllus* sp.), 3 katydids, 3 camel crickets (*Ceuthophilus* sp.), 3 noctuid moths, 1 larva of a moth; 10 voles (*Microtus ochrogaster*), 6 white-footed mice (5 *Peromyscus leucopus* and 1 *P. maniculatus*), 4 harvest mice (*Reithrodontomys megalotis*); 1 shrew (*Cryptotis parva*); 4 snakes (3 *Thamnophis sirtalis*, 1 *Storeria dekayi*); 4 lizards (2 *Eumeces obsoletus*, 1 *Cnemidophorus sexlineatus*, 1 *Ophisaurus attenuatus*); 4 frogs (*Rana pipiens*), 1 tree-frog (*Hyla versicolor*).

Records from the Harvey County, Kansas study area include a series of 69 food items from 55 stomachs (of living snakes) and 210 food items from 113 scats. There is a relatively high proportion of vertebrates, including some frogs, in the stomachs, and with no frogs but more miscellaneous insect material in the scats. But, for the sake of brevity, the two categories of items are combined in the following list: 55 grasshoppers (12 unspecified, 1 "locustid," 31 "oedipines," 7 "tryxalines," 5 "locustines," 2 *Melanoplus bivittatus* and one each of *M. femur-rubrum*, *M. scudderi*, *M. differentialis*, and *Arphia simplex*); 48 crickets (31 *Gryllus assimilis*, 17 unspecified); 14 katydids (11 *Daihinia brevipes*, one each of rhadiphorine, conocephaline and *Neoconocephalus* sp.); 9 noctuid moths and 1 moth larva; 26 miscellaneous insects (including 13 "beetles," 1 elaterid, 1 curculionid, 1 lygaeid bug, 1 ant, 1 wasp); 1 spider, 7 mice (5 *Peromyscus maniculatus*, 2 unspecified), 4 unidentified mammals, 1 vole (*Microtus ochrogaster*), 1 shrew (*Cryptotis parva*), 84 lizards (77 *Cnemidophorus sexlineatus*, 6 *Sceloporus undulatus*, 1 unspecified), 6 snakes (4 "natricines," 1 *Thamnophis* sp., 1 *Pituophis melanoleucus*), 1 "reptile," 1 "bird," 9 frogs (4 unspecified, 1 *Rana catesbeiana*, 4 *Rana pipiens*, 1 *Rana* sp., 1 *Pseudacris triseriata*).

Kinds of Prey

Throughout the range of the racer small mammals make up an important portion of the food, and the bulk of those eaten are voles (*Microtus* sp.) and white-footed mice (*Peromyscus* sp.). The voles being diurnal, and having habitat preferences similar to those of the racer, are especially subject to attack, but only large adult racers are capable of swallowing a full grown vole. Probably most of the voles eaten are immature. Of the white-footed mice, *P.*

maniculatus especially prefers a grassland habitat, and is usually found in situations frequented by the racer. Being mainly nocturnal and crepuscular, it is usually in hiding at times when the racer is prowling, but may be flushed from its nest in a shallow burrow or beneath a sheltering object, and overtaken by the snake. Other mammals that are important in the food are harvest mice and other mice, shrews, and young cottontails. The latter are small enough to be eaten by racers only in the early stages of their life in the nest before weaning. Rats (*Rattus, Sigmodon*), moles, sciurids, and weasels are less frequent prey, ordinarily too large to be eaten by racers and taken chiefly as defenseless juveniles.

Predation on birds is relatively uncommon, and in most instances it involves the eggs or nestlings, or fledglings still slow and clumsy and incapable of sustained flight, or, occasionally, injured adults. Nests that are vulnerable are chiefly those of ground nesting species, or of kinds that nest near the ground in grass or thickets. Many of the birds recorded have not been identified to species, but those identified have included a variety of small passerines and also domestic chicks.

Lizards figure prominently in most of the food samples, but only a few species, those that live on or near the ground in grassy places, have been recorded. Most of the records pertain to scaly lizards (*Sceloporus undulatus* and *S. graciosus*), earless lizards (mainly or entirely *Holbrookia maculata*), racerunners (*Cnemidophorus sexlineatus*) and skinks (*Lygosoma laterale* and *Eumeces* sp.).

Snakes are important in the racer's food in most parts of the range, but the large racers of the Northeast are those most inclined to ophiphagous habits. The common garter snake (*Thamnophis sirtalis*) is the species most commonly eaten. Probably this is a matter of availability rather than preference, since the garter snake is one of the commonest and most widely distributed of North American snakes, occurring throughout most of the racer's range. The green snakes (*Opheodrys*) also are represented frequently. The other snakes eaten are mostly medium-sized to small colubrids, of a variety of kinds. However, there are three records (from Connecticut, Missouri and Kansas) of the racer preying on the venomous copperhead. There are many records of the racer preying on smaller individuals of its own species. In my own records racer remains appeared 18 times, equalling in frequency those of the common garter snake and exceeding all other kinds. In four of these instances the scale remains were relatively few and the

scales were relatively large, suggesting as an alternative to actual predation that a racer may have eaten part of its own sloughed skin, or that patches of shed skin may have adhered to the scat after its deposition in the trap. However, in the remaining 14 instances the remains of racer found in scats clearly indicated cannibalism, since the scales found were small and numerous and often were associated with bone. Cannibalism seems to occur frequently enough to be a significant factor in the reduction of the first year young. Liner (1949:230) described two instances of cannibalism in a litter of blue racers hatched in captivity. In one instance two young had seized the same lizard, and one having swallowed the lizard, continued to engulf the other snake, although it was of a size approximately equal to that of the first snake. Nevertheless, swallowing was completed, with the snake eaten pressed in a series of curves. A second instance of cannibalism occurred when one young racer attempting to catch a lizard struck another racer by mistake, then retained its hold and commenced swallowing. A similar instance was observed in a brood that I kept in 1962 after hatching had occurred in the laboratory.

Hatchling turtles of two kinds (*Chrysemys picta, Terrapene carolina*) have been reported in the racer's food. Probably other kinds are eaten also. However, the awkward shape and almost inflexible shell of the prey on the one hand, and the slender form of the racer, with limited distensibility of the gullet on the other, would limit this type of predation to occasional instances involving an unusually large racer and a small turtle.

There seem to be no records of the racer preying on salamanders. Many kinds of frogs are eaten, chiefly ranids and hylids, and the leopard frog (*Rana pipiens*) is the most frequent victim. Wright and Bishop (1915:160) stated that the toad (*Bufo terrestris*) occupied first place in the racer's food in the region of Okefinokee Swamp, Georgia, but they mentioned no specific instances of this species being eaten. Klimstra (*loc. cit.*) found only four toads in his large sample of digestive tracts from Illinois. Because of their virulent dermal secretions, bufonid toads are avoided by many kinds of snakes and predation on them by the racer probably is unusual.

Most authors who have written concerning the food habits of the racer have mentioned insects as part of the diet. Statements in the literature have often seemed to imply that the racer feeds on insects in general, according to their availability. However, the large number of records now available demonstrate that the racer

is highly selective in choice of its insect food, that soft-bodied orthopterans, chiefly crickets, grasshoppers and katydids, are the usual insect prey, with occasional predation on moths and their larvae. Eating of other insects such as cicadas and June beetles, is a rarity, but on occasion a racer may be tempted to sample such prey when it finds the newly emerged imago before its exoskeleton has hardened. I am convinced that such rarely occurring items as carabid beetles, hemipterans, homopterans, diplopods and spiders are secondary prey items, eaten by frogs that later were eaten by the snakes, in most instances if not in all. It is noteworthy that several of the same genera of grasshoppers and crickets are prominent in the food samples collected in widely separated parts of the racer's range.

As might have been anticipated, different species of prey were not utilized by the racers to the same extent throughout the snakes' season of activity. Grasshoppers, for instance, fluctuated from a low of 25. 3 per cent (frequency) in the May sample to a high of 41.4 per cent in the September sample. Availability of prey, rather than any change of preference on the part of the racer, explains this trend. Thus, the locust, *Arphia simplex,* which, unlike most local grasshoppers, overwinters in the adult stage, is most prominent in the food in May, represented by 15.7 per cent, but it decreases progressively to a low of 1.8 per cent in September. The common grasshoppers of the genus *Melanoplus* show just the opposite trend, increasing during the summer, from a low of 2.62 per cent in May (when all are nymphs and most are too small to constitute a meal worthy of a racer's attention) to a high of 31.5 per cent in September. Mammals are best represented in the food in May, when they collectively comprise nearly 30 per cent of the items taken, and they are progressively less well represented as the summer advances. Both *Microtus* and *Peromyscus* conform to this trend, but the relative numbers of *Peromyscus* rise again abruptly in October. The general trend may be explained by the fact that in May most small mammal populations have a high proportion of young of the year, and these young are especially vulnerable to predation by the snakes. Also, insects in general are less available in spring, and this may force the racers to utilize vertebrates to a greater extent than at other seasons. Actually, the seasonal changes in food sources are not especially striking, and it seems that each important prey species is utilized more or less throughout the season of the racer's activity.

TABLE 5. DISTRIBUTION BY MONTHS OF VARIOUS CATEGORIES OF PREY ITEMS RECORDED FROM BLUE RACERS FROM KANSAS, CHIEFLY FROM THE RESERVATION AND ROCKEFELLER TRACT

	May	June	July	Aug.	Sept.	Oct.
Cricket (233)	.17	.37	.28	.01	.05	.12
Ceuthophilus (94)	.01	.19	.30	.14	.13	.23
Katydid (96)	.03	.06	.08	.25	.15	.43
Melanoplus (188)	.03	.12	.27	.15	.19	.24
All grasshopper (388)	.15	.17	.21	.16	.12	.19
Microtus (79)	.45	.32	.13	.02	.07	.01
Peromyscus (39)	.41	.18	.08	.08	.05	.20
All mammal (162)	.41	.25	.14	.03	.05	.12
Lizard (70)	.07	.46	.29	.15	.01	.02
Snake (61)	.37	.18	.08	.13	.09	.15
Arphia (72)	.50	.25	.12	.04	.03	.06

TABLE 6. DISTRIBUTION OF VARIOUS COMMON PREY ANIMALS IN A SAMPLE OF 625 AMONG RACERS OF DIFFERENT SIZE GROUPS

SNOUT-VENT LENGTH (MM.) OF RACERS IN SAMPLE	200 to 299	300 to 399	400 to 499	500 to 599	600 to 699	700 to 799	800 to 899	900 to 999	1000 to 1099
Kinds of prey and their percentage frequencies in samples: gryllid cricket	.40	.39	.11	.25	.23	.15	.15	.12	.08
Melanoplus		.09	.14	.14	.14	.15	.20	.27	.25
Ceuthophilus	.20		.11	.13	.06	.07	.12	.09	.04
Orchelimum				.04	.02	.01	.01	.01	
tettigoniid			.03	.02	.06	.03	.02	.05	
"other grasshopper" and miscellaneous orthopteran		.30	.25	.10	.09	.03	.12	.07	.09
Arphia simplex			.03	.02	.05	.08	.08	.04	.09
miscellaneous insect		.04	.04	.09	.07	.04	.08	.05	.04
lizard	.20	.09	.18	.09	.07	.11	.01	.01	
snake	.20		.07	.06	.05	.04	.05	.08	.12
Microtus			.04	.02	.08	.13	.09	.12	.25
Peromyscus		.09		.02	.05	.06	.03	.05	.04
"other mammal"				.01	.04	.10	.03	.03	
bird							.01	.01	
Total prey items for size group	5	23	28	101	120	121	127	76	24

The wide disparity in size between young and adult racers also results in utilization of different food sources to some extent. In some kinds of snakes adults and young draw their food from entirely different sources, but in the racer there is broad overlap, as shown in Table 6. The samples from the largest and smallest size groups of racers are relatively small. Two important kinds of prey —voles and grasshoppers of the genus *Melanoplus*—were not found at all in the smallest size groups of snakes and comprised increasing percentages in the food of the larger size groups. A large adult vole is too large to be swallowed except by an unusually large racer, and a young vole old enough to leave its nest is far too large for a hatchling racer. Grasshoppers of the genus *Melanoplus* are relatively large and heavily armored, and so are relatively immune to attacks from the smaller snakes. Small soft-bodied orthopterans including *Gryllus, Ceuthophilus* and *Orchelimum,* and also lizards and snakes, are best represented in the food of the smaller racers. Other types of prey showed no definite correlation with size of the racer taking them.

Reproduction

Sexual Behavior

Many observers have published accounts of the courtship and/or mating of the racer, but all of these are, to some degree, incomplete. Because of the widely different circumstances, and the different viewpoints of the observers involved, the several accounts give much different impressions of sexual behavior in this species. Either singly or combined, the published accounts do not provide an adequate description of the process.

My own observations, made both under natural conditions and in large outdoor enclosures, are likewise somewhat incomplete, but indicate that the whole sequence of courtship and mating is divisible into the following well-defined stages: 1) the finding of a receptive female by the male; 2) the persistent following of the female by the male, who courts her by lying extended along her body and performing writhing movements, with periodic interruptions during which he momentarily leaves the female and courses rapidly through the grass around her; 3) the acceptance of the male by the female, signalled by the raising of her tail and the almost instantaneous intromission; 4) the dragging of the passive male by the female while he is firmly attached to her during the period of coitus; 5) separation of the pair and involution of the male's hemipenis.

Even in the breeding season, racers that were confined in enclosures usually were either indifferent to each other or responded with reactions of fear or hostility. In moving they tended to follow the edges, and often two moving in opposite directions would approach each other; when this occurred, one snake might strike at the other with a short jab that seemed to be mostly bluff, and then would dart away. The males, being smaller, were usually the more wary.

Sexual behavior was noticed on only a few occasions. Several large adult males were less wary than others and usually manifested curiosity or interest toward other racers. My most complete observations of sexual behavior were made on May 18, 1962, when a newly caught adult male was added to an enclosure of 100-foot circumference already containing several racers, two of which were large adult females. Within half an hour the male was found courting one of the females. She was lying in a loose coil, with the male extended along her. At my approach the female darted way in alarm for approximately three feet, and the male moved with her, so swiftly and adroitly that he maintained contact and was in approximately his original position with respect to the female when she stopped.

Spasmodic rippling movements passed down the body of the male as he lay in contact with the female. These movements lasted several seconds, increasing in intensity, alternating with longer periods of little or no movement. As each period of vigorous writhing reached its climax, the male's head jerked forward and backward several times in seeming excitement. The female's behavior was mostly passive. She seemed to be receptive, but from time to time, without any noticeable warning, she darted away for several feet as she had when the pair was first discovered. Each time the male darted forward with her, maintaining contact while she moved. These swift movements of the female seemed to be spontaneous, at least in most instances there was no evident cause for alarm. The female's movements seemed to stimulate the male's interest rather than to discourage him. In most instances the female moved only four to five feet, then stopped abruptly or turned back. She would stop in a loose resting coil, in thick grass, with the male lying over her. Often she coiled in such a way that the posterior end of her body was beneath her forebody, but this did not seem to deter the male from moving the posterior end of his body into position beside hers. After a sudden change in the

female's position, the rear of the male's body would perform groping movements along that of the female until his cloacal region was approximately opposite hers. The male sometimes had his chin pressed against the female's back, especially when he was moving forward along her, but more often his head was raised, and freqently was as much as 18 inches from the female's head.

At intervals averaging approximately ten minutes, during a little more than an hour of observation, the male would suddenly dart away from the female, and with unusually rapid and animated movements, he would move around her in an irregular and devious course, sometimes as far as five feet away, but usually within 18 inches. Usually on each such expedition several or many circuits were made; then the male would return to the female and would glide rapidly along her until he attained the mating position. A period of especially vigorous courting movements would follow.

At 12:55 p. m. it was necessary for me to discontinue observations, and I left the female confined in a cloth bag. Returning at 1:20 p. m. I found that the male was not displaying interest in the female confined in the bag, nor in the other female loose in the enclosure. The first female was released from the bag, and was out of sight for approximately four minutes. When relocated she was again attended by the male, who was carrying on courtship even more vigorously than he had before. At 1:35 p. m. the male achieved intromission. Although the pair was under observation at the time intromission occurred, the actual eversion of the hemipenis was not seen because the snakes were partly concealed by dense vegetation. There was a sudden flurry of movement, the male's head waving and his body thrashing. In an instant these violent movements subsided, and after a few seconds the female began to crawl forward slowly. The male had relaxed, and relinquished his contact with the female anteriorly. As she moved away he was dragged after her tail-first. He made slight backward wriggling movements that perhaps aided in maintaining sexual contact. The female's restlessness increased, and in eight minutes she dragged the male in a circuitous course a distance estimated to be between 20 and 30 feet. At 1:40 p. m. the pair was ten feet from the point where copulation had begun. The female showed increasing inclination to climb, raising her head and forebody against the trunks of saplings, and finally reaching up one to a branch 20 inches above the ground, and climbing first along the branch and then farther up the main trunk. As she progressed the

male was lifted from the ground, dangling limply suspended by his hemipenis and its base had become exposed. At 1:43 p. m. separation occurred and the male dropped into the grass. Semen dripped from the cloacae of both snakes. That from the female was tinged with blood. The individuals involved in this observation were kept in the enclosure subsequently but no further sexual behavior was noted.

Contrary to the popular belief that these racers have permanent mates, all available evidence indicates that they are promiscuous, and two or more males may simultaneously court the same female in the brief spring breeding season. On May 24, 1960, while I was walking in a hilltop field of brome grass, a sudden movement attracted my attention to three racers lying alongside each other. Only the posterior parts of their bodies and their tails were visible. Two were males and were performing the characteristic slow writhing movements against the body of the female from either side. Although the heads were not in view, the snakes may have been able to see me through the screening vegetation; after I had watched for approximately 20 seconds, all three suddenly took alarm, for no apparent cause, and scattered.

Further evidence of promiscuity is provided by the account of Ellicott (1880:207) who wrote regarding the eastern subspecies: "I noticed a ball of black snakes (*Bascanion constrictor* L) rolling slowly down a steep and stony hillside . . . about two miles above Union Factory, Baltimore County, Md. . . . kept together by procreative impulses." It was stated that this observation was made in early spring. "Snake balls" have often been observed, and described in the literature; usually the snakes involved were garter snakes (*Thamnophis*) or water snakes (*Natrix*). Seemingly, typical aggregations consist of a single adult female and several or many males attempting to mate with her. There is a distinct possibility that the snakes involved in Ellicott's observations were misidentified.

Sexual behavior of the racer is in most respects remarkably similar to that of the common garter snake, *Thamnophis sirtalis*, well known through the work of Blanchard and Blanchard (1942). In studying sexual behavior of racers, several observers have failed to differentiate between the different stages of the mating process, and have assumed that copulation was occurring when actually only the precopulatory behavior was observed. In an early description of courtship in this racer in Kansas, Brons (1882:365) stated

that the female "at times, seems to toy with the male, indisposed to yield to his importunities, though pressed with ardor. To avoid his suit, at times, she will dart through grass, among stones, or enter a crevice. Should he be able to reach his mate while within a hole, he is not slow in bringing her to the surface, again to be repulsed. Upon an unbroken ground the sexual union is less prolonged. Here she is unable to free herself from his quick and effectively directed moves. In case she attempts to quit him, a coil is thrown about her body, and his head laid flat upon her neck, and replaced as promptly as dislodged, evidently in the endeavor to propitiate her."

Another account probably based on courtship rather than copulation is that of Wright and Wright (1957:135), who described the behavior of a pair of *C. c. priapus* on Billy Island, Okefinokee Swamp in southern Georgia, on May 8, 1921, as follows: "They were stretched out, more or less coiled . . . the rear parts of the bodies from the vent were entwined. The female, or smaller one seemed to have its tail around that of the male. There were contortions or quiverings from time to time. . . . May 8, 1921: Jackson Lee saw black snakes entwined, the male seizing the female by the top of the neck."

Blanchard and Blanchard (*op. cit.*) have described the dragging of the male by the female during coitus in the garter snake, and the temporarily inseparable bond formed between members of a pair by the recurved spines of the engorged hemipenis, but it has not been generally recognized that the process is much the same in other colubrines. Cottam (1937:229) described and photographed mating in a pair of *C. c. mormon* in Utah. The copulating racers were shown in a loose coil lying alongside each other with tails intertwined. However, when disturbed by the observers, these racers made frantic efforts to escape, crawling in a spiral course, while remaining attached and intertwined, "with no evident attempt to separate" during approximately a quarter hour of observation.

The racer is notorious for its aggressive behavior and occasional alleged attacks on humans in the breeding season. The tendency has doubtless been much exaggerated, especially in the verbal second- or third-hand accounts based on the alleged observations of eye-witnesses. Nevertheless, the supposition that large adults will sometimes pursue or attack humans when disturbed is well substantiated. In most of the instances known to me, it is the large eastern subspecies, *C. c. constrictor,* involved in these incidents, and

seemingly the smaller racers of the Middle West, far West and South are less inclined to behave aggressively. In May 1958 two pairs of large racers were confined in a semicircular wire enclosure thirty feet across and open on top, and with natural vegetation, at the Reservation headquarters. Often in approaching the cage I saw two or more racers in close association, but because of sheltering vegetation, and the snakes' timidity observation was difficult. On May 19 a pair were lying partly extended in loose coils, but immediately the female took alarm and darted away, breaking loose from the male; his hemipenis was exposed, and underwent involution and retraction in approximately 30 seconds. Unlike the female, the male on this occasion did not attempt to escape, but turned to face me with a show of aggressiveness. Probably copulation was in its final stages when the disturbance occurred.

Circling of the female racer by the male from time to time in the course of courtship has not been recognized by previous observers as a part of the mating pattern, but Pope (1944:171) described somewhat analogous behavior, probably modified by unnatural conditions of captivity and the crowding of many racers in one cage. Pope, citing earlier observations by Noble, wrote: "When sexually excited, the male blacksnakes dash wildly about before paying court to individual females. In captivity these dashes excite all specimens confined together. A male, after picking out a mate, moves his chin lightly along her back, while undulations run forward along his sides and he extends his tongue now and then. Later he throws the part of his body near his vent over the corresponding part of the female, the two tails sometimes becoming loosely intertwined."

Recorded dates of mating for the species are all in spring, but indicate a span of many weeks for the breeding season, and this spread results in part from geographical differences. Published records are as follows:

Subspecies *constrictor*
May 12, 1930, in Ohio (Conant, 1938:55)
Subspecies *priapus*
May 8, 1921, in Georgia (Wright and Wright, 1957:135)
May 9, 1921, in Georgia (Wright and Wright, 1957:135)
Subspecies *flaviventris*
May 3, 1931 (two pairs) in Missouri (Boyer and Heinze, 1934:195)
April 18, 1936, in Missouri (Anderson, 1942:210)
May 12, 1928, in Kansas (Gloyd, 1928:123)
Subspecies *mormon*
June 10, 1927, in Utah (Cottam, 1937:229)
July 7, 1938, in California (Cunningham, 1959:17)

In the course of my live-trapping, I occasionally found more than one racer in a trap. As might be expected from the low yield per trap, such double or multiple captures were relatively rare. Chance, and unusually strategic placement of certain traps were doubtless contributing factors. May and October, being the most productive months for trapping, yielded a high proportion of these combined captures. Some involved an adult and an immature snake, or two adults of the same sex. Eliminating all these, there remain 44 heterosexual captures of adults. These latter captures are significantly concentrated in their seasonal distribution and indicate a spring breeding season; 34 were in May, six were in June and four were in October. Eight of the May records and one June record each involved a trio of snakes—two males and a female in every instance. Distribution of the spring records, grouped in five-day intervals, was as follows:

May 11 to May 15: 14	June 5 to June 9: 0
May 16 to May 20: 5	June 10 to June 14: 2
May 21 to May 25: 8	June 15 to June 19: 2
May 26 to May 30: 13	June 20 to June 24: 0
May 31 to June 4: 1	June 25 to June 30: 1

Approximately 87 per cent of the records fell in the twenty-day interval, May 11 to 30, which is regarded as the main breeding season. Presumably males continue to be at the peak of breeding condition and continue to search for females after the latter have become unreceptive, partly explaining the scattering of records through most of June.

Several of the females found in traps with males in May had abundant active sperm in their cloacae and oviducts and probably had been inseminated within a few hours of the time they were checked. Others lacked sperm, but the cramped quarters inside the traps may have effectively prevented the consummation of courtship, especially when two males were confined with the same female. None of the females trapped with males in October was found to be inseminated, and it seems doubtful whether copulation ever occurs at that time of year, although males have motile sperm and seem to be in breeding condition then.

Cycle of the Male

Cloacal smears indicate that males mature sexually and first produce sperm in August and September when they are a little more than a year old. Insofar as could be determined, there was no sexual activity at this time of year, and actual breeding of the

adolescent racers was postponed until the following May. By this time at an average age of 20 months, the snakes had made further growth.

Mr. Dwight R. Platt studied the changes in the male reproductive organs during the annual cycle at Harvey County. In racers recently emerged from hibernation he found the seminiferous tubules filled with Sertoli syncytium, but containing few germ cells. Spermatogonia proliferate in May and June. During the first half of July primary spermatocytes are the dominant cells in the seminiferous tubules. By early August spermatids are dominant and the first free spermatozoa are present. In late October spermiogenesis is essentially complete and the tubules are relatively empty before the snakes hibernate. During the season of activity the seminiferous tubules increase to approximately double their minimum diameter, reaching the maximum in August. Cyclic changes

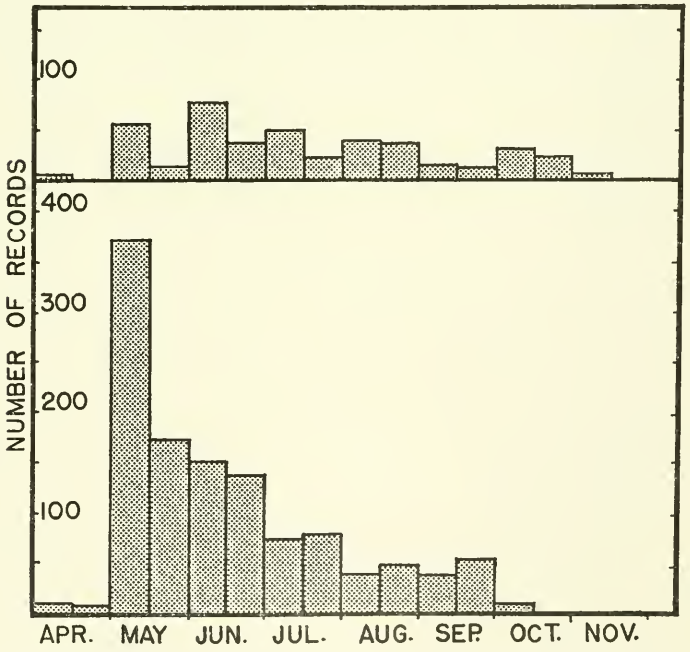


FIG. 16. Catches, in semi-monthly periods, of racers in their summer habitats, at Harvey County Park (upper) and at Reservation and Rockefeller Tract (lower). Intensive activity in spring (the breeding season), tapering off rapidly as the season advances, is well shown by the larger sample, but in the years of trapping at Harvey County Park operations usually were not fully underway until the latter part of May.

in size and secretory activity of the ductus deferens, ductus epididymis, and sexual segment of the renal tubules occur, with maximum size and secretory activity coinciding with the time of movement and storage of the spermatozoa. The latter are stored in both ductus deferens and ductus epididymis. Despite the short breeding season, a male racer has active sperm at all seasons.

Eggs

In accounts of the racer in the humid southeastern United States, Brimley (1903:261), Wright and Bishop (1915:160) and Tinkle (1959:195) mentioned the ease with which the eggs might be found and the superficial situations in which they were sometimes deposited. Both Wright and Bishop, and Tinkle made field studies in swamps, where presumably the subsoil was saturated with moisture and too wet for the eggs. Tinkle mentioned finding one clutch beneath a discarded newspaper and another beneath a small, thin board. Surface (1906:167) stated that in Pennsylvania the eggs were to be found in loose soil, in sawdust piles, or in decaying wood of hollow logs or trees. Clark (1949:249) stated that in northern Louisiana the eggs are laid in soft, moist soil such as may be found beside decaying logs. Minton (1944:457) found two clutches under flat stones on hillsides in Indiana. In the more arid climates of the far western states the species' habits are much different in this regard. Through many years of familiarity with *C. c. mormon*, I have never seen its eggs. Presumably nests in this part of the range are deep underground, most often in old burrows of the pocket gopher (*Thomomys*), which are so abundant that in many areas the soil is riddled with them. Burrows of the ground squirrels (*Spermophilus* sp.) and other small digging mammals also provide potential insulated nest sites with the favorably moderate temperatures and high humidities that the eggs of snakes require.

On the morning of July 10, 1962, I was directed to the sites of two clutches recently plowed up, 1½ miles north of the Reservation (Pl. 21, Fig. 2). The eggs were in a fallow field having a stand of sunflowers three to five feet high. The plow blades turned the soil at a depth of approximately seven inches. In each instance only a few eggs were visible. They were well scattered in the loose soil turned up by the plow; 21 were found in one clutch and 10 in the other. All the eggs were intact except two that had minute punctures from which liquid oozed. Seemingly the eggs *in situ* had been well above the level of the blade—at depths of four to five

inches. No nest cavities were discernible where the eggs were found, but elsewhere in the field tunnels of moles (*Scalopus aquaticus*) and prairie voles (*Microtus ochrogaster*) were exposed by the plow. Presumably the eggs had been in such tunnels, which had disappeared as the loose soil crumbled. Another clutch was discovered in an adjoining field on July 16. The nine eggs were at depths ranging from 6½ to nine inches, and only the two topmost eggs had been turned up by the plow. All three clutches were within a few feet of the edges of the fields.

On the Reservation and nearby areas I have seen remains of an estimated 20 clutches that have been destroyed by predators. The remains in every instance consisted of an excavation, and the strewn torn and empty eggshells. Nests were at depths of four to eight inches in old tunnels, which most often seemed to be those of moles but also included some of the prairie vole, and perhaps some of the pine vole (*Microtus pinetorum*). All these nests were in open sunny places in prairie or pasture habitat.

Many observers have described the eggs of the racer, which are white, elliptical, somewhat elongate, with tough, leathery, somewhat flexible, shells, and a granular surface. Like other snake eggs, those of the racer gradually absorb moisture during incubation. They become more turgid and increase in weight and dimensions, especially in breadth, and by the time of hatching are nearly twice their size at laying. Between different clutches and even within the same clutch there is notable variation in the size of the newly laid eggs. Munro (1948:199) noted that in a small adult racer

TABLE 7. NUMBERS AND SIZES OF EGGS IN CLUTCHES OF THE BLUE RACER FROM EASTERN KANSAS

NUMBER OF EGGS	Lengths (mm.)	Widths (mm.)	Weights (grams)	Snout-vent length of female (mm.)
17	26.5(29–24)	17.0(19.0–16.5)	5.5(6.0–4.4)	892
8	33.3(39–31)	16.3(17.5–14.0)	6.0(6.7–5.6)	899
12	29.1(32–25.5)	17.1(18.5–16.0)	4.9(5.2–4.4)	773
14	26.9(30–24)	19.2(20–18)	5.2(6.2–4.4)	772
10	31.7(33–29)	16.5(18–15)	6.0(6.5–5.6)	807
11	29.7(33–27)	16.7(18–15)	5.4(5.8–5.0)	858
21	28.9(32–27)	18.4(19.5–18)	5.9(6.3–5.6)	1038
13	30.7(34–28)	19.3(20–18)	6.8(7.5–6.1)	907
18	29.0(30–26)	17.9(19–16)	4.9(5.5–4.3)	911
12	30.3(34–28)	17.8(19–15)	5.2(6.1–3.8)	843
14	30.9(36–29)	19.4(21–18)	6.8(7.6–6.2)	846

kept by him, the eggs laid were larger but less numerous than those produced by a large adult. Munro noted also that shape of eggs in the two clutches differed; the smaller snake produced more elongate eggs of smaller diameter. The idea that eggs laid by the smaller females are more slender and elongate is not supported by my own data. For 11 clutches of eggs examined soon after laying, dimensions, weights, and the lengths of the females are shown in Table 7.

In a clutch of eggs beginning to hatch on September 3, 1958, dimensions and weights were as follows: length 31.8 (36-30), diameter 22.0 (24-21), weight 9.7 (10.3-9.3).

Gravid females that were kept in captivity in anticipation of their laying usually produced their clutches within a few days. The laying dates of such individuals are shown in the following list. Those with asterisks were from the Harvey County study area, others were from the Reservation and Rockefeller Tract.

June 19, 1961	July 1, 1961	July 12, 1961
June 21, 1959	July 4-5, 1962*	July 15, 1961*
June 23, 1961*	July 6, 1955	July 18, 1961*
June 26, 1959	July 7, 1959*	July 20, 1961
June 29-30, 1962*	July 7, 1959*	August 3, 1960*

A further indication of the period when laying occurs was provided by the appearance of females gravid and progressively more swollen with eggs, then their abrupt disappearance and replacement by thin and wrinkled individuals that obviously were recently parturient. The following records show the course of these events on the Reservation in the years when summer trapping was done with sufficient consistency. These dates provide a rough approximation of the time when laying occurs locally. They indicate a laying season concentrated in a period of approximately three weeks in this locality. Records from published literature also indicate that laying occurs in late June and early July at the latitude of Kansas, but somewhat earlier in the southern United States.

TABLE 8. DATES WHEN PARTURIENT AND GRAVID RACERS WERE CAPTURED ON RESERVATION AND ROCKEFELLER TRACT IN SEVERAL YEARS, INDICATING TIME OF OVIPOSITION

YEAR	1958	1959	1960	1961	1962
First parturient female	June 18	June 17	June 22	June 20	June 13
Last gravid female	July 8	July 11	July 5	July 12	July 16

Many authors have made statements regarding the size of the clutch in the racer, on the basis of those found in the field, those laid after capture, or those dissected from gravid females. Some of the statements were based upon small but unspecified samples, and are far from the mark. From records accumulated in the course of my own field work, and a summarization of those in published accounts a substantial sample is available showing the usual size of clutch in the area of my study, and the trends of geographic variation in some parts of the range.

C. constrictor (all combined)
151 clutches averaged 10.61 (2 to 31) eggs.
C. c. constrictor ..... 14 clutches averaged 16.80 (7 to 31) eggs.
C. c. priapus ..... 11 clutches averaged 12.60 (7 to 21) eggs.
C. c. mormon ..... 43 clutches averaged 5.79 (2 to 13) eggs.
C. c. flaviventris ..... 82 clutches averaged 11.78 (5 to 26) eggs.
C. c. stejnegerianus, one clutch contained 10 eggs.

In the foregoing list the sample of *C. c. flaviventris* may be divided as follows:

Reservation and vicinity: 36 clutches averaged 11.65 (6 to 21) eggs.
Harvey County study area: 21 clutches averaged 12.0 (5 to 18) eggs.
Museum specimens from Kansas: five clutches averaged 9.2 (6 to 14) eggs.
Published records (Kansas, Indiana, Iowa, Louisiana, Missouri, Oklahoma, Texas): 20 clutches averaged 12.5 (5 to 22) eggs.

TABLE 9. PUBLISHED RECORDS INDICATING DATES OF LAYING IN DIFFERENT POPULATIONS OF COLUBER CONSTRICTOR

DATE OF LAYING	Subspecies	Area	Authority
June 9, 1952	*flaviventris*	SE Texas	Guidry (1953:50)
July 1–2, 1920	*flaviventris*	Texas	Ortenburger (1928:183)
June 1, 1920	*flaviventris*	Texas	Ortenburger (1928:183)
June 9, 1926	*flaviventris*	Oklahoma	Force (1930:31)
June 24, 1926	*flaviventris*	Oklahoma	Force (1930:31)
July 19, 1928	*flaviventris*	Oklahoma	Force (1930:31)
July 16	*flaviventris*	Oklahoma	Carpenter (1958:114)
July 4–5, 1948	*flaviventris*	Kansas	Munro (1948:199)
July 4, 1948	*flaviventris*	Kansas	Munro (1948:199)
June 26, 1930	*flaviventris*	Ohio	Conant (1938:55)
July 3, 1961	*mormon*	NW Oregon	Van de Velde, Martan and Risley (1962:212)
June 7, 1957	*priapus*	S Illinois	Rossman (1960:219)
June 19, 1912	*priapus*	S Georgia	Wright and Bishop (1915:160)
July 10, 1940	*priapus*	S Illinois	Cagle (1942:187)
July 6	*constrictor*	New York	Ditmars (1907:284)
June 27–July 5, 1951	*constrictor*	Virginia	Werler and McCallion (1951:251)
June 5, 1947	*stejnegerianus*	S Texas	Auffenberg (1949:54)

Published records of clutches laid by racers, from which figures used in the foregoing account were obtained, include the following:

C. c. constrictor: 22 (Barbour, 1950:104); 21, 13 (Brimley, 1903:261); 25 (Conant, 1938:55); 8 (Ditmars, 1907:284); 7, 12, 14, 16, 19, 20, 31 (McCauley, 1945:76); 14 (Wright and Wright, 1957:136).

C. c. flaviventris: 7 (Anderson, 1942:210); 22 (Brumwell, 1951:205); 11 (Carpenter, 1958:114); 8, 9, 9 (Force, 1930:31); 10 (Guidry, 1953: 50); 18 (Liner, 1949:230); 5, 8, 17 (Marr, 1944:484); 5, 14 (Munro, 1948:199); 13, 19 (Ortenburger, 1928:183); 6, 15 (Tinkle, 1959:195); 15, 19 (Wright and Wright, 1957:141).

C. c. priapus: 20, 21 (Cagle, 1942:187); 7 (Conant, 1938:55); 19 (Rossman, 1960:219); 5, 9, 11, 14 (Wright and Bishop, 1915:160); 16 (Wright and Wright, 1957:147).

C. c. mormon: 13, 9, 8, 5, 5, 5, 4, 4 (Cunningham, 1959:17); 5, 6 (Stebbins, 1954:374); 6 (Van de Velde, Martan and Risley, 1962:212); 3, 6 (Wright and Wright, 1957:144).

C. c. stejnegerianus: 10 (Auffenberg, 1949:54).

In general, the number of eggs in the clutch is proportional to the size of the female producing them. The larger and bulkier females produce more eggs. Geographic trends in number of eggs produced are perhaps controlled by differences in size between different populations; thus, the large eastern *constrictor* produces nearly three times as many eggs per clutch as does the small western *mormon,* whereas the centrally located *flaviventris* is somewhat intermediate in size and in numbers of eggs produced.

In most reptiles growth in length and bulk continues after attainment of sexual maturity. For many kinds including *Eumeces fasciatus, Crotaphytus collaris, Cnemidophorus sexlineatus, Agkistrodon contortrix* (Fitch, 1954:60; 1956:236; 1958:36; 1960:174), and *Sceloporus olivaceus* (Blair, 1960:94), it has been shown that the larger and older females in a population produce more offspring than do the smaller and younger individuals. This situation applies in the racer, as shown by the clutches of 52 females correlated with their sizes and presumed ages (Fig. 17, Table 10). The two-year-olds contribute a relatively small quota to the annual brood, partly because their clutches are small, but more especially because many of them fail to attain sexual maturity in time to breed. Many of the female racers that are more than two years old also fail to produce an annual clutch of eggs. The 24-day period May 28 to June 20 inclusive is judged to comprise the period when eggs have generally enlarged sufficiently to be detected in gravid females, but still have not been laid in most instances. In this period, in 1960, 1961 and 1962, ratios of gravid females to those

not detectably gravid in several supposed age groups arbitrarily established on the basis of size, were as follows:

Two-year-olds	2 gravid,	13 apparently not gravid
Three-year-olds	5 gravid,	4 apparently not gravid
Four-year-olds	3 gravid,	2 apparently not gravid
Five-year-olds	4 gravid,	3 apparently not gravid
Six-year-olds (or older)	8 gravid,	2 apparently not gravid

From the appearance of these snakes it is reasonably certain that none had already laid eggs when it was recorded, but there is some

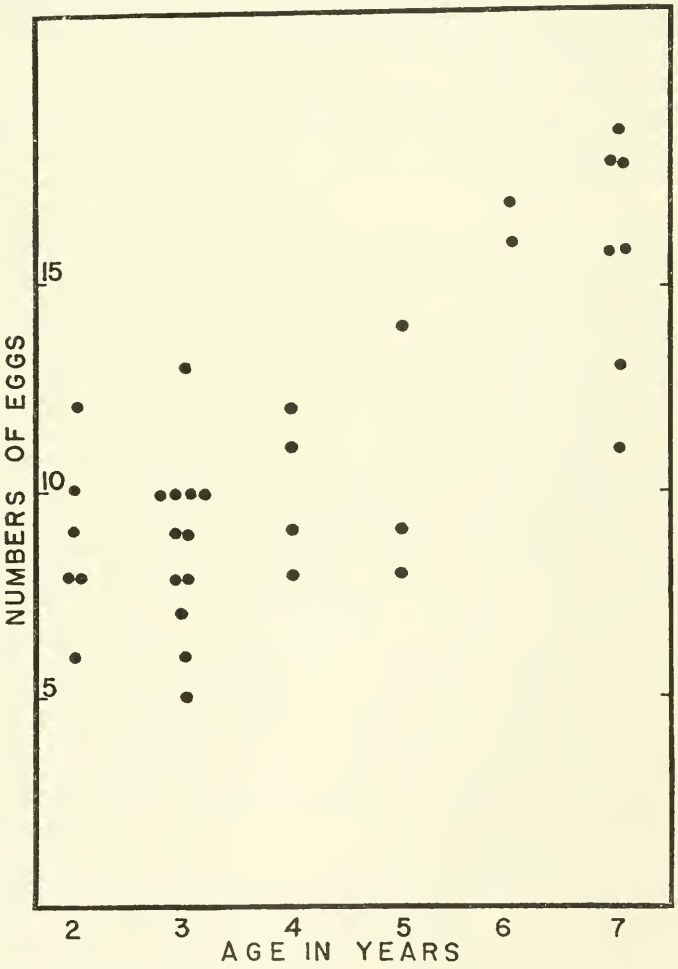


FIG. 17. Graph showing number of eggs per clutch, and correlation with supposed age (as deduced from length of body) in female blue racers from the Reservation, Rockefeller Tract, and Harvey County Park.

possibility that a few individuals not noticeably gravid at the times they were examined, produced eggs subsequently. However, these meager data do seem to indicate that most of the two-year-old females and a minority of older individuals fail to produce clutches in the annual breeding season.

TABLE 10. FECUNDITY OF FEMALE RACERS IN VARIOUS AGE-SIZE CLASSES, ALL FROM THE RESERVATION AND ROCKEFELLER TRACT

MOST PROBABLE AGE IN YEARS OF FEMALES (AS INDICATED BY SIZE)	Number of females in sample	Snout-vent length of females; average and extremes	Number of eggs in clutch
2.....	10	688 (589–748)	9.2 (6–12)
3.....	19	789 (756–840)	9.9 (5–14)
4.....	7	856 (850–861)	10.8 (8–12)
5.....	6	907 (892–933)	13.0 (8–17)
6 or more....	10	1005 (955–1088)	15.7 (11–19)

Under unfavorable conditions eggs can be resorbed, but probably this can occur only if initiated before ovulation. A racer in which six small eggs were palped on June 28, 1960, was kept until July 23 but did not oviposit. It no longer appeared gravid and the ova could not be detected by palpation. Another female had 13 eggs on June 21, 1960, but by July 23 when the snake was released the eggs had not been laid and no longer could be detected. Both snakes refused to feed throughout their confinement.

Like other reptilian eggs, those of the racer are dependent upon the warmth of their surroundings for incubation. They are tolerant of a wide range of environmental temperatures, but the higher the temperature the more rapidly incubation proceeds. Under natural conditions there may be much difference in hatching time in two clutches laid at the same time and in the same locality. Site of the nest—deep and well insulated, or shallow; in a well shaded situation or one exposed to maximum amounts of sunshine—would largely control rates of development. Clark (1949:249) writing of the subspecies *anthicus* in north-central Louisiana, stated: "eggs are laid about the first of June. . . . young begin to make their appearance at about . . . July 1." Even for the southern states these dates of laying and hatching seem somewhat too early to reconcile with the records published by other observers, and are in need of verification, especially since they seem to be based upon vaguely remembered observations rather than upon written records. At the other extreme Surface (1906:167) wrote of *constrictor* in

Pennsylvania that hatching may occur as late as October, and that there is evidence some young may even remain in the egg over winter before hatching occurs. Several incubation periods are on record for clutches laid and hatched in captivity, as follows:

C. c. mormon, Oregon, 47 and 51 days (laid July 3, 1961, hatched August 19 and 23; Van de Velde, Martan and Risley, 1962:212).

C. c. stejnegerianus, Texas, 73 days (laid June 5, 1947, hatched August 17, Auffenberg, 1949:54).

C. c. priapus, S. Illinois, 58 and 59 days (laid July 10, 1940, hatched September 6 and 7, Cagle, 1942:187).

C. c. flaviventris, Kansas, 50 days (laid July 4 and 5, hatched August 23 and 24; Munro, 1950:124).

C. c. flaviventris, Texas, 43 days (laid June 9, 1952, hatched July 22; Guidry, 1953:50).

No incubation periods for eggs in natural nests have been recorded. In the course of my study, eggs obtained from 12 captive females were hatched in confinement, with an average incubation period of 51 days (43 to 63) as follows:

Laid July 6, 1955, hatched August 20.
Laid July 3, 1958, hatched September 3 and 4.
Laid June 21, 1959, hatched August 17.
Laid June 26, 1959, hatched August 17.
Laid July 7, 1959, hatched August 23 to 25.*
Laid June 23, 1960, hatched August 20.*
Laid June 30, 1961, hatched August 30.
Laid July 15, 1961, hatched September 1 and 2.*
Laid July 18, 1961, hatched September 2 and 3.*
Laid July 4 and 5, 1962, hatched August 15 and 16.*
Laid June 29 and 30, 1962, hatched August 14 and 15.*
Laid July 6, 1962, hatched August 16 to 20.*

In the foregoing list those entries marked with asterisks were obtained from the Harvey County study area; all others were from the Reservation and Rockefeller Tract.

Hatching

Detailed observations on hatching were made on a clutch of eggs laid on June 29 and 30, 1962, by a female caught in Harvey County. The first egg in the clutch had already been laid in the trap when the female was found at 11:30 a. m., June 29. Two of the eggs were abnormal, with thin transparent shells, and were found to lack embryos when they were opened on July 7. Later, two other eggs were attacked by mold and the embryos died early in development. The clutch was kept in a can of slightly damp soil. At 2:30 p. m. on August 13, when the clutch was examined, egg no. 6 was found to have hatched. The young snake had made a 21-millimeter slit in the shell. At 12:50 a. m. on August 14, it was discovered that eggs 1, 4, 5 and 7 each had been slit. No. 4 had two parallel slits separated by a two-millimeter strip of shell, and the young racer

could be seen inside. At 1:05 a. m. this young snake had changed position and was lying upside down in the egg, his snout protruding slightly through one of the slits. At 1:45 a. m. he was again right side up, still in the shell. At this time each of the slit eggs showed the protruding snout of a young snake. Occasionally the viscous liquid egg white would be blown into a large bubble on the surface of the shell as the young snake exhaled. A third slit, parallel to the others, had appeared in egg no. 4. A hatchling emerged from egg no. 1 between 2:20 and 3:20 a. m., and another from no. 7 between 7:00 and 9:00 a. m. The hatchling struck vigorously many times, and vibrated his tail when he was disturbed. Egg no. 3 was first slit between 7:00 and 9:00 a. m., and three more slits appeared in it between 9:15 and 10:15 a. m. At 12:45 p. m. a hatchling was found in the act of emerging from egg no. 4, and approximately the anterior one-fourth of its body protruded. Disturbed by the movements of the observer, the little snake drew back into its shell. This hatchling began to emerge again at 12:50 and his hatching was completed at 1:00 p. m. Between 5:40 and 6:20 p. m. a hatchling emerged from egg no. 3 (for several hours this hatchling had been lying on its back inside the egg, with only its snout protruding); two slits appeared in egg no. 2 and three slits appeared in egg no. 8. At 6:50 p. m. the hatchling in the latter thrust his snout through the slit in this eggshell. This hatchling was lying on its back at first but by 10:50 it had shifted to a normal position. It emerged from the shell between 2:35 and 2:50 a. m. Egg no. 2 was the last to hatch. At 7:05 p. m. the hatchling inside made two additional small slits in the shell, and at 7:30 p. m. thrust its snout through one of them, while lying on its back. At 1:45 a. m. it was right side up, but at 3:00 a. m. had reverted to its previous position. At 4:40 a. m. it was again right side up, and it emerged from the shell at 5:55 p. m.

On August 17, at 11:00 a. m., hatchlings no. 5 and no. 6 had lost their egg teeth. All others still had their egg teeth then, but by 10:00 p. m. that of no. 8 was missing, and that of no. 4 was loose and dropped out while the snake was being handled. On August 20 at 9:00 a. m., hatchling no. 7 had lost its egg tooth; nos. 2 and 3 retained theirs only in part, and no. 1 had its egg tooth intact. By noon on August 22 no trace of an egg tooth remained on any of the hatchlings.

In the same group of hatchlings sign of impending molt was first noticed on the morning of August 17, when no. 6 was noted to have

its eyes clouded and milky in appearance. By evening no. 1 had attained the same stage and no. 7 was beginning to show it. On the morning of August 20, shedding had begun in no. 6, while no. 2 and no. 8 had milky eyes. The eyes had cleared in no. 1 and no. 7, and were still clear in the remaining hatchlings. On August 22 shedding had been completed by no. 1 and no. 8, and all others were in the process of shedding.

Another clutch of 14 eggs from a recently captured female was found freshly laid in a cage on July 6, 1962. Hatching of 13 occurred August 16 to 20, as shown in Table 11.

Growth

Hatching usually occurs in late August or early September, and the disparity in size between hatchlings and adults is greater than in some other kinds of snakes. In 76 young from ten clutches of eggs incubated in the laboratory, averages and extremes for measurements and weights were as follows: snout-vent length, 214.5 (186 to 244) millimeters; tail, 59.3 (44 to 73) millimeters; weight, 4.16 (2.4 to 5.8) grams. In each brood the size tended to be fairly uniform, except that there were usually one or more stunted individuals markedly smaller than the others. However, there were striking differences in size between the young of different broods. None of the young captured was as small as the average hatchling from the clutches incubated in captivity, but in the 14 years of my study only four young were captured in August. The hatchlings

TABLE 11. TIMES OF HATCHING IN A CLUTCH OF RACER EGGS FROM HARVEY COUNTY PARK

NUMBER OF EGG	Time at which shell was slit by hatchling		Time that hatchling emerged	
	Day	Hour	Day	Hour
1	Aug. 17	10:50 a.m.	Aug. 18	3:00 to 6:00 p.m.
2	Aug. 17	12:15 to 12:50 p.m.	Aug. 18	3:25 to 4:25 p.m.
3	Aug. 17	1:40 p.m.	Aug. 17	10:45 p.m.
4	Aug. 18	3:00 to 6:00 p.m.	Aug. 19	before 7:00 a.m.
5	Aug. 16	10:45 a.m.	Aug. 17	6:30 to 7:55 a.m.
6	Aug. 17	9:00 a.m.	Aug. 18	6:30 to 7:30 a.m.
7	Aug. 17	4:15 p.m.	Aug. 20	1:00 to 7:00 a.m.
8	Aug. 17	3:40 p.m.	Aug. 18	5:00 to 6:00 p.m.
9	Aug. 17	7:30 p.m.	Aug. 18	6:30 to 7:30 a.m.
10	Aug. 16	10:48 a.m.	Aug. 17	11:05 a.m.
12	?	no record	Aug. 18	6:00 to 6:30 a.m.
13	Aug. 17	8:00 to 8:20 a.m.	Aug. 17	5:30 to 5:50 p.m.

are relatively secretive and elusive, and the lush vegetation of late summer provides them with abundant hiding places. Nevertheless it is remarkable that the hatchlings are so seldom seem, when their probable abundance is taken into account.

Probably all of those captured had already made some growth after hatching. By early November or the last week of October, racers have almost or quite completed their season of activity, and are at the hilltop ledges, preparing to hibernate, if they have not already retired into dormancy. For 25 young of the year captured in this period at the end of the growing season, measurements and weights were as follows: snout-to-vent, 327 (273 to 418) millimeters; tail 93 (72 to 114) millimeters; weight, 12.3 (7 to 19) grams. In the ten-week period between hatching and hibernation these young had already passed through their period of most rapid growth, having added, on the average, more than 50 per cent to their original lengths, and almost tripled in weight. In these young about to enter their first hibernation, variation in size and weight is much greater than in the hatchlings; some have fared much better than others, and there are significant age differences. Within any one year the time of hatching is spread over several weeks because of differences in the time of laying, and differences in nest sites, with variation in heat received, which promotes or delays the rate of incubation. Year to year differences in the trend of weather increase the dispersion as the incubation time is shortened in hot, dry summers and lengthened in those that are relatively cool and moist.

TABLE 12. GROWTH OF FIRST-YEAR RACERS

SEX	Original record			Record(s) of recapture		
	Date	Snout-vent length, millimeters	Weight, grams	Date	Snout-vent length, millimeters	Weight, grams
♂	Aug. 17, 1959	223	5.3	Sept. 12, 1960	503	42
♀	Oct. 26, 1959	278	10	Oct. 26, 1959	566	55
♀	Nov. 2, 1959	340	18	May 11, 1961	582	65
♀	Nov. 10, 1959	348	13.7	June 20, 1961	733	127
♀	Oct. 19, 1952	361	15.3	Oct. 9, 1953	620	68
♂	May 9, 1953	368	17	May 13, 1954	609	84
♀	April 16, 1950	328	142	Oct. 10, 1950	603	78.2
♀	May 17, 1956	358	15.2	Oct. 6, 1956	575	52
♂	Nov. 1, 1953	330	11	May 21, 1955	674	92

Though covering a wide size-range, the young of the year entering hibernation are still a distinct size group, not yet overlapping that of the next older group of young. Growth during the first year of life is best shown by the individuals in Table 12, all of which were marked either before their first hibernation or soon after emerging from it, and were recaptured either the following autumn, or in spring soon after emerging from a second hibernation.

These records indicate that the young racers at the time of their second hibernation have grown to a snout-vent length of well over 500 millimeters, but less than 700 millimeters, and a weight of more than 40 grams but less than 100 grams. Other racers marked in the first few weeks of life were recaptured after two or more seasons of growth, and indicate the sizes that may be expected in young adults from two to five years old, as shown in Table 13.

TABLE 13. GROWTH OF RACERS MARKED AT AN AGE OF LESS THAN ONE YEAR AND RECAPTURED IN THEIR SECOND, THIRD OR FOURTH YEARS

Sex	Original record				Record(s) of recapture			
	Date	Snout-vent length in mm.	Weight in grams	Probable age in months	Date	Snout-vent length in mm.	Weight in grams	Probable age in months
♂	Nov. 12, 1952	342	....	2½	May 20, 1955	702	110	33
♂	Nov. 1, 1953	330	11	2	Aug. 16, 1956	780	162	35½
♂	Nov. 12, 1953	293	....	2½	May 14, 1956	634	96	32½
					Oct. 13, 1956	689	110	37½
♂	April 15, 1955	320	13	9½	June 8, 1958	740	118	45
♂	Oct. 2, 1955	348	18	1	May 22, 1958	728	120	33
					May 21, 1960	795	130	57
♂	June 25, 1959	378	10	10	June 30, 1960	590	60	22
					June 7, 1961	705	123	33
♂	Nov. 1, 1953	330	11	2	Aug. 25, 1957	805	183	48

Unlike young of the year, racers in their second autumn were trapped in large numbers. By this time all were large enough to be caught in the traps of quarter-inch wire mesh, and they were the most abundant size group. Many that were marked at this stage were recaptured after intervals of months or years, showing the trend of growth. Some of these snakes in their second autumn already had overtaken the more retarded third-year individuals.

The two age classes cannot be separated with certainty. Selected records of individuals that were almost certainly second-year young at the time they were marked are presented in Table 14.

TABLE 14. GROWTH OF YOUNG RACERS THAT WERE MARKED NEAR THE TIME OF THEIR SECOND HIBERNATION

Sex	Original record				Record(s) of recapture			
	Date	Snout-vent length in mm.	Weight in grams	Probable age in months	Date	Snout-vent length in mm.	Weight in grams	Probable age in months
♂	Oct. 6, 1960	595	80	13	July 23, 1961	650	70	23
♂	Oct. 13, 1950	525	52.6	13½	Oct. 2, 1951	675	105	25
♂	Nov. 2, 1950	545	55.6	14	Oct. 24, 1951	670	100	26
♂	Sept. 2, 1957	522	57	12	Oct. 14, 1958	690	103	25½
♂	Oct. 17, 1953	558	47	13½	May 10, 1955	718	.....	32
♂	Nov. 14, 1956	587	57	14½	May 20, 1958	728	100	52½
					June 17, 1959	880	219	64½
♂	Sept. 7, 1959	533	45	12	June 6, 1961	740	112	33
♂	Oct. 17, 1959	558	56	13½	July 21, 1960	625	63	22½
					June 7, 1961	670	95	33
♂	Oct. 16, 1952	577	62.0	13½	May 31, 1955	809	160	45
					May 11, 1956	855	144.3	56½
♂	Oct. 11, 1950	570	65.9	13½	July 11, 1956	820	193.6	82½
♂	Oct. 14, 1953	560	52	13½	June 29, 1958	794	256	70
♂	Oct. 6, 1950	563	55.8	13	Sept. 28, 1958	907	243	109
♂	Oct. 14, 1953	523	44	13½	May 19, 1959	818	190	80½
					May 17, 1960	850	211	92½
♂	Oct. 13, 1953	521	50.1	13½	May 13, 1958	814	166.4	44½
					June 3, 1959	826	165	47
♂	Nov. 5, 1953	512	34	14	May 22, 1958	847	135	69
♀	Aug. 11, 1953	534	39.2	11½	Sept. 18, 1954	670	143	24½
♀	Oct. 14, 1949	588	55.2	13½	Oct. 11, 1950	713	114.0	25½
♀	Oct. 6, 1950	570	60.4	13	Oct. 11, 1951	783	174	25½
♀	Oct. 31, 1953	582	58	14	Oct. 5, 1954	860	195	25
♀	Oct. 21, 1959	588	63	13½	May 7, 1961	730	120	32
♀	May 14, 1960	506	34	20½	Oct. 26, 1960	690	90	26
♂	Oct. 22, 1960	527	45	13½	Oct. 7, 1961	620	74	25
♂	May 3, 1960	530	48	20	May 16, 1961	700	110	32½
♂	May 27, 1961	535	40	21	Oct. 25, 1961	672	98	26

From the records in Table 14 and many more like them, average and extreme sizes for progressively older age groups were estimated. Even racers that were already of adult size when they were marked were tentatively identified with one or another age group, and their records of subsequent growth were used. Most of the

records show that the females grow more rapidly than the males, and are, on the average, larger at any given age.

Relatively few individual racers were recaptured after periods of several years. Each of the eight listed in Table 15 is among those that were captured in four or more different years, and their records are significant in revealing the trend of growth after sexual maturity has been attained. These snakes, one to three years old at the time they were marked, show well the persistent but decreasing growth, and the fluctuating weight that is characteristic of this and other species.

Some of the largest racers recorded had already reached unusually large size when they were first captured, so there was no opportunity to determine their ages. Several others, originally captured as small- or medium-sized adults, subsequently grew to a size approaching the maximum, and thus provided a basis for

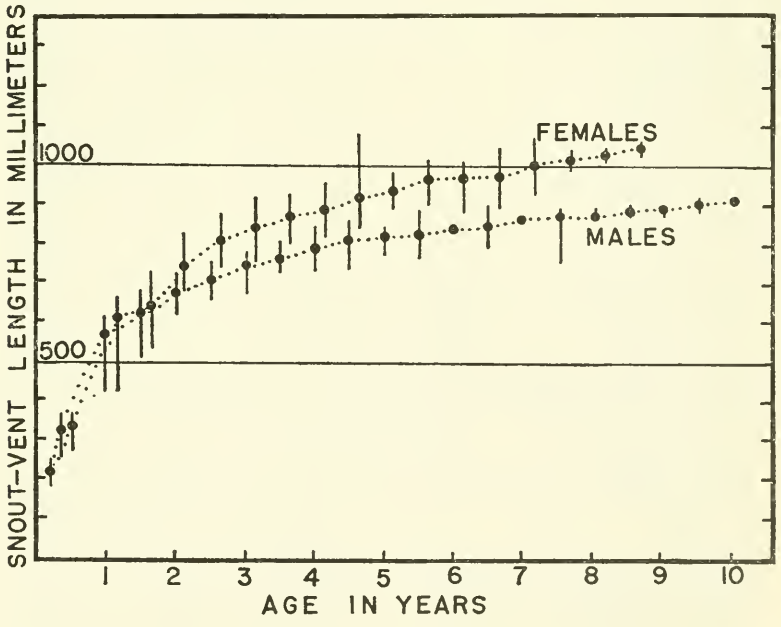


FIG. 18. Graph from records of blue racers marked early in life and recaptured, showing average and extreme snout-vent lengths for males and females of various ages. Growth is especially rapid in the first year, but continues, with gradual slowing, throughout life. In hatchlings, the sexes are of approximately equal size, but females grow to be markedly larger than males.

TABLE 15. CHANGES IN LENGTHS AND WEIGHTS IN EIGHT RACERS RECAPTURED REPEATEDLY OVER PERIODS OF YEARS

DATE OF CAPTURE	Snout-vent length in millimeters	Tail length in millimeters	Weight in grams	Probable age in months
No. 1, male				
October 21, 1953...	676	216	85	25½
October 12, 1954...	733	238	128	37½
July 31, 1955.....	755	243	143	46
May 20, 1956.....	785	250	153	55½
July 15, 1957.....	788	252	162	69½
June 30, 1958.....	820	264	200	81
May 15, 1959.....	828	263	195	91½
May 14, 1960.....	840	265	195	103½
No. 2, male				
May 9, 1955.....	678	212	105	32
May 26, 1958.....	827	248	195	69
May 3, 1959.....	865	262	218	80
May 14, 1960.....	877	264	218	92½
July 16, 1960.....	890	257	190	94½
No. 3, male				
May 26, 1955.....	565	171	53	21
August 28, 1957....	798	245	155	48
May 13, 1958.....	814	249	137	56½
May 4, 1959.....	848	252	180	68
June 12, 1961.....	896	262	198	93½
No. 4, male				
May 19, 1956.....	632	208	78	20½
August 2, 1957.....	740	238	123	35
May 20, 1959.....	796	246	132	56½
May 23, 1960.....	813	280	140	68½
No. 5, male				
June 30, 1956.....	594	188	73	22
October 12, 1956...	658	200	80	27½
July 14, 1957.....	690	220	102	34½
June 23, 1958.....	749	226	136	46
July 24, 1959.....	751	239	133	59
May 27, 1960.....	765	235	130	69
No. 6, male				
October 19, 1956...	518	167	43	13½
July 19, 1957.....	673	218	96	22½
May 5, 1960.....	780	250	175	56
May 9, 1961.....	840	272	272	68
No. 7, female				
May 12, 1957.....	790	238	175	32½
September 3, 1957..	810	243	208	36
October 1, 1958....	883	259	206	49
July 11, 1959.....	915	247*	190	58½
September 12, 1960	930	249*	238	72½
September 14, 1961	1012	268*	332	84½
No. 8, female				
June 23, 1955.....	601	175	67	22
August 3, 1958....	920	255	300**	60
July 23, 1959.....	955	281	211	71
May 18, 1960.....	962	262	260	81

* Incomplete. ** With food.

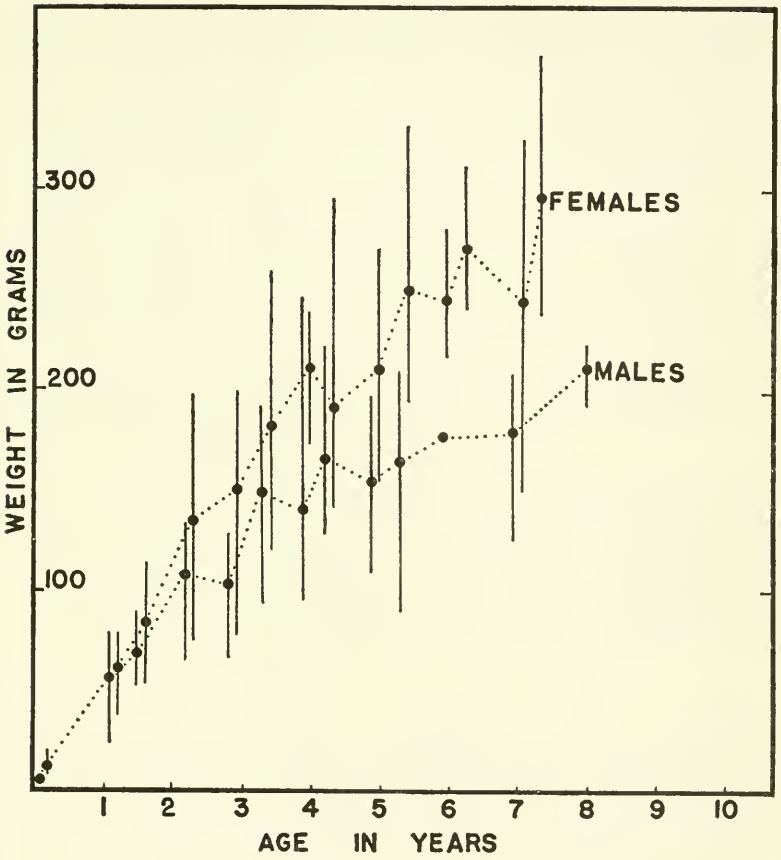


FIG. 19. Graph from records of blue racers marked early in life and recaptured, showing average and extreme weights in samples of different ages. Early in life the females outstrip males in growth and the size differential increases throughout life.

estimating the ages of large individuals. The records of nine such racers are listed in Table 16.

A few adult racers recaptured, including different individuals of small, medium, and large size, failed to make any measurable gain in length over periods of months, or even over several years. Most often the large individuals were those that failed to grow or made only slight gains. Some of the snakes that failed to increase in length suffered dramatic weight losses, perhaps as a result of injury, disease, or parasitism. However, other individuals that failed to gain appreciably in length did gain in weight. Doubtless both

TABLE 16. GROWTH IN SEVERAL RACERS THAT WERE ALREADY ADULT WHEN ORIGINALLY CAPTURED AND THAT SUBSEQUENTLY ATTAINED UNUSUALLY LARGE SIZE

Sex	Original record				Record(s) of recapture			
	Date	Snout-vent length in mm.	Weight in grams	Probable age in months	Date	Snout-vent length in mm.	Weight in grams	Probable age in months
♂	May 14, 1956	815	191	56½	May 15, 1959	905	243	92½
					May 16, 1961	945	287	104½
♂	May 22, 1958	825	251	68½	June 25, 1959	840	205	82
					May 27, 1960	880	210	93
					Oct. 14, 1961	900	223	109½
♂	May 19, 1959	705	105	32½	May 28, 1960	828	.....	45
					July 3, 1961	900	265	58½
♀	Nov. 6, 1954	823	190	38	June 30, 1958	1030	350	82
♀	June 6, 1955	810	190	33	May 21, 1959	1087	345	80½
♀	Aug. 29, 1957	885	265	48	Aug. 6, 1960	1041	235	83
♀	May 1, 1958	633	84	20	May 30, 1961	1088	320	57
♀	July 20, 1958	862	203	46½	June 30, 1960	1020	238	70
♀	Oct. 18, 1956	845	185	37½	May 20, 1958	905	240	56½
					Oct. 22, 1959	1085	375	74

genetic and environmental factors were involved. A few racers gave the impression of being stunted by adversity. All records obtained of growth (or failure to grow), throughout the period of my study were used in compiling Table 17.

Mortality Factors and Adaptations for Survival

Defense, and Escape

The behavior patterns that are associated with defense and escape in snakes are widespread. The common racer is typical of the more generalized snakes. Almost all elements of the racer's behavior are found in snakes of other genera and perhaps, of other families. The racer differs from these only in minor details of its behavior, in the circumstances under which various behavioral traits are elicited, and their relative importance. The common racer is one of the swiftest of North American snakes, and it usually depends upon speed to avoid enemies. Racers crossing roads may detect approaching automobiles at a distance, and thereby may be stimulated to accelerate their movements and so escape onto the

shoulders rather than becoming traffic casualties as many individuals of most other kinds of snakes do under the same circumstances. The chances of such escape are of course much better on dirt roads that are relatively narrow and have a rough surface permitting efficient traction, than on wide smooth, paved highways. The snakes are somewhat reluctant to venture onto open expanses of pavement.

A racer suddenly startled by close approach of a human usually flees at high speed. The first part of its course, up to 20 feet or more, is marked by a violent lateral thrashing of the body and tail, which may help the snake to gain speed, but which seem chiefly

TABLE 17. SIZES OF RACERS OF DIFFERENT AGE GROUPS IN MAY AND OCTOBER

AGE IN YEARS	Males				
	Snout-vent length in mm.			Weight in grams	
	Average	Typical range	Observed range	Average	Observed range
1+	539	432–609			
2—	615	500–676	560–674	68.2	51–92
2+	668	610–700	620–710	107.4	63–134
3—	706	677–730	648–755	102.1	65–129
3+	740	701–754	667–780	147.0	93–216
4—	757	731–772	725–809	139	95–251
4+	785	755–793	720–850	167.4	128–225
5—	805.5	773–810	743–855	152.4	110–198
5+	810	801–831	773–858	163.9	89–211
6—	827	811–831	765–883	175.9	130–230
7—	845	832–850	788–900	181.2	125–210
8—	868	851–873	740–890	217.5	194–225
8+	870	861–884			
	Females				
1+	581		415–658		
2—	644	520–739	580–738	83.5	52–127
2+	743	685–804	670–826	135.2	73–200
3—	810	740–829	730–880	149.4	98–219
3+	836	804–869	736–915	181.2	120–268
4—	866	830–880	791–920	212.3	175–243
4+	883	870–914	810–952	191.2	143–300
5—	914	880–929	833–1088	209.6	136–275
5+	932	915–954	883–990	250.4	195–336
6—	965	930–961	892–1020	245.9	218–283
6+	970	955–980	885–1003	271	243–336
7—	974	962–990	919–1050	251.3	150–330
7+	1000	980–1015	930–1085	295.6	235–375

designed to draw attention of a potential attacker to the spot that the snake is leaving. In any event, the mode of progression abruptly changes to a swifter and much smoother travel, and the snake may seem to vanish completely or as it glides rapidly away, its course may be marked by the slowly waving tops of tall grass. The trend of travel away from the site of disturbance is in an irregularly zig-zag course. The method of crawling, with lateral undulations of the body, supported against scattered pivot-points along the way, tends to prevent the snake from moving more than a short distance in a straight line.

In checking traps along hilltop rock ledges in October, I have often flushed racers that had come to the ledges searching for hibernation dens. In such an instance the startled racer would usually dart away down the steep slope at unusually high speed, and within a few seconds might have covered 100 feet or more, progressing with a minimum of lateral undulations, and seeming to flow or coast over the ground surface with scarcely any effort. Although coursing downhill in this manner provided an effective method of escape, racers startled at the ledges or on other sloping ground sometimes followed a course parallel to the ledge, or even turned uphill, with disastrous slowing. Often I have accomplished capture by hand, by the strategy of running downhill to get below the escaping snake, causing it to turn back up the slope, there to be slowed to the extent that it could be overtaken.

A racer that has been flushed, and has disappeared after creating a commotion by its violent thrashing, may, within a period of minutes, return surreptitiously to the vicinity, gliding back slowly and silently from the direction opposite that in which it departed. It may climb into a tree or bush where, lying stretched on outer twigs and concealed in dense foliage, it will sometimes permit close approach, rather than reveal its presence by moving. If too much disturbed however, such a snake will move away, higher, or to the opposite side of the clump, with a slow and stealthy gliding motion which is likely to escape detection. The sudden stops and abrupt changes in direction make it difficult to follow the course of a climbing racer, even though it is moving slowly. The tendency to climb to escape danger seems to be especially strong in the western subspecies, *C. c. mormon.* In my years of experience with the racers in the chaparral belt of western Oregon and California, I found that one of the most characteristic responses to danger was to climb into a bush or low tree and seek concealment in the thick foliage.

In most instances the snake was from one to eight feet above the ground; usually it did not attempt to climb high in a tree even when there was opportunity to do so. The racer's prowess as a climber is limited. In thick brush where its weight is supported by numerous stiff twigs simultaneously, it is at home and can travel rapidly, but it cannot cling effectively to rough bark of a vertical tree trunk as can the rat snakes (*Elaphe* sp.) and others that are more specialized in their arboreal adaptations. Chaparral-type shrubs such as *Ceanothus cuneatus* and *Arctostaphylos viscida* were those in which western yellow-bellied racers were seen climbing most frequently. Crab-apple (*Pyrus ioensis*) and haw (*Crataegus* sp.) were the shrubs most frequently utilized by blue racers on the Reservation. Carr (1950:80) noted that Florida racers were much less given to tree-climbing than were those of more northern regions. *C. c. stejnegerianus* of southern Texas is reputed to have arboreal tendencies highly developed (Mulaik and Mulaik, 1942:14).

The racers kept in an outdoor enclosure in the summer of 1962 spent much of their time above the ground, climbing in several walnut saplings. Usually in the warmer part of the day three or four of the five racers in the pen were climbing. In the trees a racer usually lay extended or in a loose coil among foliage in the outer twigs, at a height of five to 12 feet. Such a snake might rest for hours in almost the same position. Racers do not ordinarily enter the water voluntarily, but they are swift and efficient swimmers when the need arises. On one occasion a large female, seen near the edge of the pond on the Reservation, and approached from the landward side, took to the water without hesitation and swam strongly to the opposite shore more than 100 feet away. Other observers have recorded similar incidents.

A racer that is suddenly startled at close range may make no attempt to escape, but instead may coil and perform slow writhing movements, with the head pressed to the ground and concealed beneath part of the body. Musk, exuding from the anus is spread over the body surface as the movements continue. Only a small percentage of the racers found free in their natural habitats reacted in the manner described. In each such instance, the circumstances were such that the racer was prevented from making its usual rapid getaway, either because temperature was unusually low for activity, or because the snake was away from suitable cover. After removal from a live-trap, with handling, and especially clipping of

scales, racers were much more likely to behave in this passively defensive manner, which seemingly constitutes a second line of defense in snakes which have been prevented from escaping—either cornered, captured, or injured by a predator. The musk is creamlike in color and consistency, and is secreted from sausage-shaped glands in the base of the tail. Its odor is rather disagreeable, but less so than that of musks of various other genera. Also, it is less penetrating and lasting than many other musks. In handling the racers removed from traps I attempted to avoid being smeared with the musk by grasping the snake by the tail and neck and keeping its body stretched out. While the snake was being examined, and measured a droplet of musk would form at the anal orifice and would begin to flow down the snake's body. To avoid contact with the musk I would wipe away the droplet with a paper towel or leaf, but the musk droplet might be replaced several times within the few minutes that the snake was restrained.

A racer that is confronted with an object arousing its suspicion or indicating possible danger, may move away slowly with a characteristic "threat display." The forebody and neck are held rigid, well off the ground, and slightly arched, with the neck flattened in a vertical plane—causing this part of the snake to appear from lateral view larger than it actually is. The tongue is protruded frequently and waved slowly. A racer that has been disturbed and is trying to gain shelter in a direction that brings it closer to the danger usually will adopt this tense attitude, but a single threatening movement will cause it to abandon its circumspect pose, and panic in an attempt to reach the nearest shelter in the shortest possible time.

A common response to an alarm is to vibrate the tail. The tail being long and slender is vibrated much less rapidly than the short, muscular organ of a rattlesnake, or even the medium-short tail of a bull snake. The rapid twitching produces a characteristic sound in dry vegetation. A racer that vibrates its tail is fully active and aroused; the sound is heard as the snake pauses before it makes a dash for shelter. At times the sound probably functions as a decoy to distract the attention of potential predators, affording the racer an opportunity to escape.

A racer that is cornered or captured usually puts up a spirited struggle, striking vigorously and repeatedly at its tormentor. If only cornered, it will make slashing strokes at the enemy, jerking back to a coil from each stroke in a manner that causes the teeth

to lacerate the enemy's skin in long scratches if the stroke finds its target. The rapid recoil often causes teeth to be jerked from their sockets and left embedded in the wound inflicted by the bite. On many occasions in sustaining a bite from a racer I have received such teeth which have remained undetected for a day or more until soreness and festering led to their discovery and removal. A racer that is grasped may deliver several bites within a few seconds, chewing vigorously to imbed its teeth to the maximum at each bite.

If grasped by the tail and held clear of the ground, the racer would swing its body with a rapid whirling and twisting motion, which in a few seconds would twist off the end of the tail, unless countermeasures were promptly taken. Many racers, especially the larger and older ones, have parts of the tail missing, as a result of such escapes, and perhaps also from freezing in hibernation or from certain injuries and infections. If grasped by the body, the racer struggles with a violent lateral thrashing to break the grip of its captor, at the same time striking to bite and discharging musk, urinary wastes and feces.

Many of the racers examined bore scars from wounds that were probably inflicted by predators. A few had survived severe skeletal injuries, involving deformation of the spinal column or extensive tearing of muscle and connective tissue layers of the body wall, altering the normal body shape. A more frequent type of injury involved chiefly the integument, which had been ripped open by the teeth, claws, or bills of adversaries, despite the fact that the skin is remarkably tough and leathery. Patches of scar tissue with scales in irregular sizes, shapes and patterns characterized such injuries. The most frequently observed type of injury involved loss of part of the tail. Usually only a small terminal part was missing, but occasional stub-tailed individuals had lost as much as three-fourths of the tail.

No consistent trend of difference between the sexes in incidence of injuries to the tail was noticeable, but there was definite correlation with age. In the entire sample from the Reservation and Rockefeller Tract the percentages in each supposed age group (actually size group) lacking part of the tail were as follows: hatchlings, 2.9 per cent; one-year-olds, 9.5 per cent; two-year-olds, 15.8 per cent; three-year-olds, 14.3 per cent; four-year-olds, 15.7 per cent; five-year-olds, 23.2 per cent; six-year-olds, 30.9 per cent; seven-year-olds, 28.9 per cent; those eight years old or older, 21.1 per cent. The seeming reversal of trend in the older racers is difficult

to explain, but probably results from inadequate numbers in this part of the sample.

Although the racer's most characteristic response to any disturbance is to flee at high speed, certain individuals are inclined to behave aggressively under exceptional circumstances. Records of such aggressive behavior nearly all pertain to large individuals of the northeastern black racer (*C. c. constrictor*) in the breeding season. Cope (1900:794) wrote: "it is courageous and will sometimes attack, moving forward with the head raised from 1 to 2 feet above the ground." Ditmars (1944:13) wrote: "Occasional specimens in the breeding season . . . will actually attack . . . glide toward an intruder . . . striking madly at one's feet or legs." Woods (1944:257) quoted a 13-year-old amateur herpetologist, Leon Gonthier, regarding the latter's encounter with an aggressive black racer on May 7, 1944, as follows: "When I ran toward the snake about 20 feet away, it turned and came for me. As I bent over to catch it, the snake grabbed me by the shirt and hung on . . . held it off with a stick. It jumped twice more at me and came clear off the ground." Finneran (1948:124) describing the species' habits in Connecticut, stated: "A farmer . . . constantly warned me away from Coon Ledge during the spring, saying the snakes were breeding and would 'chase you.' This very thing happened. In 1943 a blacksnake followed me for approximately ten feet, and, in 1946, a male aggressively attacked me for a period of three minutes. There was ample opportunity for escape."

Natural Enemies

Little has been published concerning the natural enemies of the common racer. The king snake (*Lampropeltis getulus*) is notorious for ophiphagy, and doubtless preys upon the racer at times. Wright and Bishop (1915:169) wrote of the king snake in Okefinokee Swamp, in Georgia, that "all the smaller snakes suffer, and of the larger species, the blacksnake [racer] and spreading adder are the commonest prey." However, Clark (1949:252) examined 301 stomachs of king snakes of this species in Louisiana and found no racers, although many other kinds of snakes were represented, and, collectively, made up the greater part of the food.

A rat snake (*Elaphe obsoleta*) found in Leon County, Florida, on June 10, 1924, had a racer in its stomach, according to the Patuxent food habits file of the U. S. Fish and Wildlife Service. A California garter snake (*Thamnophis elegans terrestris*) was found

to have a juvenal racer in its stomach (Fitch, 1940:96). A large alligator lizard (*Gerrhonotus multicarinatus*) was found swallowing a small racer that had been confined with it in a bag (Fitch, 1935:12).

A few records of predation on blue racers by other reptiles on the Reservation and Rockefeller Tract were obtained. In 25 scats of the prairie king snake (*Lampropeltis calligaster*), there were 29 vertebrate prey items of which one was a blue racer. On September 15, 1962, an adult male prairie king snake 49½ inches in length was found to have a 27-inch yearling racer in its stomach. In 254 scats of the slender glass lizard (*Ophisaurus attenuatus*) vertebrate remains were rare, but there were scales and bones of one hatchling blue racer. Among 21 vertebrate prey items in 14 scats of the timber rattlesnake (*Crotalus horridus*) there were remains of one blue racer. Among 589 prey items of copperheads there were two juvenal blue racers (Fitch, 1960:200). In contrast to these scarce records of racers in the prey of other snakes, there were more frequent records of the blue racer preying on its own young. The 1008 food items from 479 racer scats contained remains of 16 racers, small young in most instances.

Raptorial birds are known to be important predators on snakes. Breckenridge (1944:118) reported finding remains of a blue racer in the pellet of a marsh hawk (*Circus cyaneus*). Many pellets of the marsh hawk collected on the Reservation were all found during the colder half of the year, and they contained no remains of reptiles. The same seasonal restrictions applied to the many pellets of four species of owls that were collected, and these also lacked remains of reptiles. One of the predators whose food habits have been most thoroughly investigated on the area is the red-tailed hawk (*Buteo jamaicensis*). Over the period 1955 through 1962, 1131 pellets of these hawks were collected, many from the Reservation, but more from localities scattered throughout the eastern one-fourth of Kansas. The pellets were those of nestlings and fledglings, nearly all collected from beneath the nests, in late May, June, or early July. Some 49 different nests were represented, and remains of 43 blue racers were found. In one nest which yielded a total of 191 food items, racer remains occurred 13 times, but no other nest yielded records of more than three racers, and some other species of reptiles, notably the black rat snake (*Elaphe obsoleta*) comprised much more important components of the food. Since only one meal in 26 contained remains of racers, it seems that a red-

tailed hawk would destroy only a few racers in the course of a year on its territory of perhaps half a square mile, and that its predation would not be a major factor in the racer's ecology.

That the red-tailed hawk is a natural enemy to be reckoned with throughout the racer's extensive range was demonstrated by the analysis of contents of 116 stomachs from localities well scattered over the United States and Canada. Among the 152 vertebrate prey items represented there were three racers: a juvenile *C. c. constrictor* from Stag Lake, New Jersey, October 16, 1927; a *C. c. mormon* from Weiser, Idaho, April 11, 1930, and a *C. c. stejnegerianus* from San Roman, Cameron County, Texas, in the spring of 1938. Because of the widely scattered geographical origin of these stomachs, a remarkably large number of species of prey were represented, and no one species predominated. Small mammals of the genera *Sylvilagus, Spermophilus*, and *Thomomys* comprised the most important component of the food; the only other reptile so well represented as the racer was the common garter snake (*Thamnophis sirtalis*) which likewise had three occurrences.

In June and July, 1954, a nest of broad-winged hawks (*Buteo platypterus*) on the Reservation yielded 71 prey items of which seven were blue racers. At least 19 species of prey were represented, although specific determinations were not possible in some instances. The prairie vole with eight records was the most frequent prey, and the racer and cardinal (nestlings) each had seven, while all other species were represented by fewer occurrences. Six of the racers were first-year young but the remaining one was thought to be an undersized second-year individual. Although an adult racer, especially a large one, would probably be an adversary too powerful to be killed and eaten by a broad-winged hawk, this hawk is perhaps one of the more important natural enemies of the first-year young in the eastern United States.

Further records of predation on racers by raptors were obtained from the U. S. Fish and Wildlife Service files through the kindness of Dr. Wm. H. Stickel. There were three records of such predation by red-shouldered hawks (*Buteo lineatus*) from Lunenberg, Massachusetts, May 1, 1896; Portland, Maine, March 16, 1906; and 65 miles northeast of Sarasota, Florida, June 10, 1918. There were two records of predation by broad-winged hawks from Catlettsburg, Kentucky, July 26, 1910, and Portland, Connecticut, May 18, 1912. There were four records of predation by marsh hawks on racers—Peck's Island, Maine, September 18, 1903;

Edgartown, Massachusetts, April 12, 1912; West [Tisbury?], Massachusetts, July 31, 1912; and Okanagan Landing, British Columbia, June 5, 1918. A sparrow hawk (*Falco sparverius*) from De Ranch, Wyoming, May 27, 1910, had eaten a racer, as had a barn owl (*Tyto alba*), from Franklin County, Kansas, November 16, 1922, and a crow (*Corvus brachyrhynchos,* nestling) from Onaga, Kansas, May 16, 1914.

Perhaps certain mammalian predators are even more important natural enemies than are raptorial birds, but records of predation on racers by mammals are few. Substantial samples of scats of opossums and coyotes from the Reservation have contained no remains of racers. The Fish and Wildlife Service files include a record of an opossum from Adrian, Michigan, on April 26, 1934, that had racer remains in its stomach. No racers were specifically recorded from a collection of 820 scats and 22 stomachs of raccoons (*Procyon lotor*) from Douglas County, Kansas, reported upon by Stains (1956:43), but occurrences of unidentified snake may have pertained in part to the racer. Skunks are probably more important natural enemies, but food habits data from the Reservation are lacking for the two kinds of skunks occurring there. Crabb (1941: 356) in a study of the food habits of the spotted skunk (*Spilogale putorius*) in southeastern Iowa, did not report any reptiles among the many kinds of prey found in scats. Several times in many years of residence near Medford, Jackson County, Oregon, I saw remains of racers which appeared to be victims of striped skunks (*Mephitis mephitis*). Tracks and other sign of the skunks were often noticed along a little-used road on a hillside, passing between a pasture and a hay field, with an oak grove, high weeds, and brush, bordering the road. The racers sometimes found as victims along this road were small- or medium-sized individuals. In every instance the predator had begun eating on the tail end of the snake, and later had abandoned the remains leaving the head and part of the forebody still intact. Predation had occurred at night. Skunks foraging mostly in twilight or darkness, probably find racers inactive beneath flat rocks or in shallow burrows. The skunks would be too slow and clumsy to catch the snakes in the open when they were fully active.

The funnel traps used for catching the racers also caught many other kinds of animals. Often a racer and another kind of snake were caught together, but, ordinarily, in these instances no damage to either resulted, although racers, copperheads, king snakes, and garter snakes are all known to eat each other's young. At times,

large predatory ground beetles (*Calosoma scrutator* and *Pasimachus* sp.) were so abundant that a dozen or more were caught together in a trap, and several times such groups attacked and killed and partly ate young racers caught in the same traps. White-footed mice (*Peromyscus leucopus*), deer mice (*P. maniculatus*), harvest mice (*Reithrodontomys megalotis*), short-tailed shrews (*Blarina brevicauda*), and least shrews (*Cryptotis parva*) all were caught rather frequently in the traps, and each, on one or more occasions, gnawed and killed or severely injured a racer trapped with it. The attacks probably were motivated by hunger in all instances, the snake in some instances failing to defend itself or escape because of low temperature. Occasionally such encounters might occur even under natural conditions, the mouse or shrew finding and attacking the snake while the latter was torpid and helpless in its hibernaculum or in a more superficial temporary shelter.

Disease

Relatively few of the racers examined showed signs of disease. The most common type of affliction was an infection of the skin causing cankerlike sores, chiefly on the ventral plates, sometimes on the head or tail. These were seen most often in snakes recently emerged from hibernation, but persisted later in the season in years of exceptionally wet weather. Some of the racers most severely afflicted appeared to be in debilitated condition. The causal organism was not determined, nor was it definitely determined whether this type of disease causes mortality.

Parasites

The ectoparasites of the racer are chiefly chiggers, the parasitic larvae of mites. Loomis (1956) in his study of the chigger mites of Kansas examined many of the racers captured in the early years of my field work. He checked a total of 130 racers, mostly from the Reservation, and found four different species of chiggers, all of the genus *Trombicula: T. alfreddugèsi, T. lipovskyana, T. kansensis* and *T. sylvilagi.* The common pest chigger, *T. alfreddugèsi,* parasitizes most of the species of reptiles, birds, and mammals occurring in Kansas, and it was by far the most common kind on the racers. The numbers per racer in different months were as follows: June, 81; July, 285; August, 432; September, 123; October, 15. Many of the racers were collected in the relatively cool and moist summers of 1950 and 1951. In a year of typical weather, heaviest infesta-

tions occur in early summer, June or the first half of July, and the numbers taper off rapidly in the hot but often dry weather of late July, August, September, and October. In hot, humid weather of early summer a racer may have several hundred chiggers attached to it, filling most of the areas of exposed skin between the scales. The chiggers are conspicuous because of their bright orange color. Like *T. alfreddugèsi, T. lipovskyana* was also found in large numbers on racers and is found on many kinds of hosts. Loomis (*op. cit.*:1281) recorded it from one kind of frog, one kind of toad, one kind of turtle, two of lizards, six of snakes, 19 of birds, and nine of mammals from eastern Kansas. Five larvae of *T. sylvilagi* were recorded from a racer captured in October. That kind of chigger is primarily a parasite of small mammals, and perhaps cannot develop successfully when it attaches to a snake. Unlike most other kinds of chiggers, this species is most in evidence in autumn and winter. A single larva of *T. kansensis* was found on a racer in October. This relatively rare kind of chigger has been found on several kinds of snakes and small mammals (including pocket gophers) and is known from hot and dry rocky places. Even the racers that were heavily loaded with chiggers showed no obvious ill effects, but the chiggers are potentially vectors of various diseases.

Of the many endoparasites found in racers, the lung fluke, *Neorenifer lateriporus* was the only one identified and frequently observed in my study (Stewart, 1959). This is a digenetic trematode of the subfamily Reniferinae. The racer is its specific host. The life history is still unknown, but in other members of the subfamily, all of which parasitize snakes, an aquatic snail and a frog are required as hosts at different stages of the life cycle. Presumably *N. lateriporus* has similar requirements. The two common local water snails, *Heliosoma trivolvis* and *Physa anatina*, are both potential hosts. By far the most probable frog host is the leopard frog. In wet weather of July the recently metamorphosed leopard frogs leave the water and disperse to all habitats, probably carrying with them the parasites acquired in the tadpole stage. The racers in turn probably acquire their flukes by eating the young frogs in summer. In any case, the adult racers are nearly all parasitized, but the flukes have not been found in those racers that were less than one year old. During their first few months, the racers are too small to swallow leopard frogs, even the young. The flukes have been seen in the live racers mostly in May, when most adults are infested with the flukes. Seemingly at this season the

flukes migrate forward into the mouth of the host. Probably this is the time when the flukes breed and lay eggs; if so, the eggs would pass through the digestive tract of the snake and escape with its feces. The latter are usually left in terrestrial situations unfavorable for the development of an aquatic stage, but perhaps some of the eggs are washed into ponds by heavy summer rains. In late summer and fall the flukes are not to be found in the mouths of the live snakes.

Most complete records of the flukes present in racers were kept in 1959. The following table shows the numbers of racers examined and the percentage having flukes in that year.

Ortenburger (1928:182) recorded lung flukes (*Renifer ellipticus*) from blue racers. In Maryland, McCauley (1945:76) also recorded numerous lung flukes (*Pseudorenifer* sp.) in an immature racer 490 millimeters in total length. Parker (1941:34) recorded *Neorenifer septicus* from racers collected at Reelfoot Lake, Tennessee, Greensboro, Georgia, and Kissimmee, Florida; also he recorded *N. georgianum* from racers collected at Reelfoot Lake. *N. septicus* was recorded by the same author from the water moccasin (*Agkistrodon piscivorus*) and *N. georgianum* was also recorded from the king snake (*Lampropeltis getulus*).

Cloacal smears from the racers examined usually showed an abundance of ciliate protozoans, either parasites or commensals, and occasionally nematode worms. Harwood (1933:66) examined two racers from the vicinity of Houston, Texas, and found four kinds of helminths: *Kalicephalus agkistrodontis, K. rectiphilus, Ophidascaris* sp., and *Polydelphis* sp. Each parasite was found in only one of the two snakes. McCauley (*loc. cit.*) recorded nematodes (*Physaloptera obtusissima*) from black racers in Maryland, and Ortenburger (*loc. cit.*) recorded *Physaloptera* sp. from the blue racer.

TABLE 18. SEASONAL INCIDENCE OF THE FLUKE NEORENIFER LATERIPORUS, IN MOUTHS OF BLUE RACERS ON THE RESERVATION AND ROCKEFELLER TRACT

	Apr. 15–30	May 1–15	May 15–31	June 1–15	June 15–30	July	Aug.	Sept.	Oct.
Number of racers checked.....	1	28	25	24	17	30	5	9	2
Percentage of sample having flukes.....	100	79	72	50	18	0	0	0	0

Populations

Composition

Since there is a brief annual breeding season, any local population of racers consists of a series of discrete annual age groups. The population reaches its annual maximum in early September, after undergoing sudden increase by the addition of the annual crop of hatchlings. Throughout the remainder of the year numbers of racers undergo gradual reduction as a result of the many combined mortality factors that affect them. This mortality is distributed among all the age classes, but the heaviest losses, both percentagewise and in actual numbers, are sustained by the first-year young. Being by far the most numerous group, these young suffer more mortality than all the other age classes combined. Presumably much of this mortality is concentrated in the early weeks of life, while the young are still near their minimum size; the rate of loss is gradually reduced as larger size is attained and some of the early hazards are outgrown. In the adult age classes also, the larger and older snakes live in greater security, and the rate of mortality is higher in the smaller and younger snakes. Even before hatching, the eggs are subject to heavy losses from predators, and probably from drying, flooding, and other unfavorable climatic factors. Unfortunately it was not possible to obtain definite figures on any of these losses since the eggs were never found under natural conditions and the hatchlings were seen only in relatively small numbers.

The records obtained from trapping racers in late spring and summer in fields provided a somewhat different picture of the population from the sample obtained along the ledges in autumn. In the former sample there were 400 males to 257 females, but in the latter sample there were 355 males to 379 females. I regard the summer sex ratio as a distorted one, brought about by the greater activity of the males in the breeding season. Racers are caught most easily in May, and the fact that two or more males often were trapped with the same female, while the reciprocal combinations did not occur, demonstrates the increased activity of the males in their search for mates at this season. In autumn there is no sexual activity; both sexes probably are equally active in seeking places to hibernate when they are trapped along the hilltop outcrops. The ratio of 51.6 per cent females in my sample of 734 may indicate that in the males greater activity at other seasons results in a somewhat higher mortality. This idea is borne out by

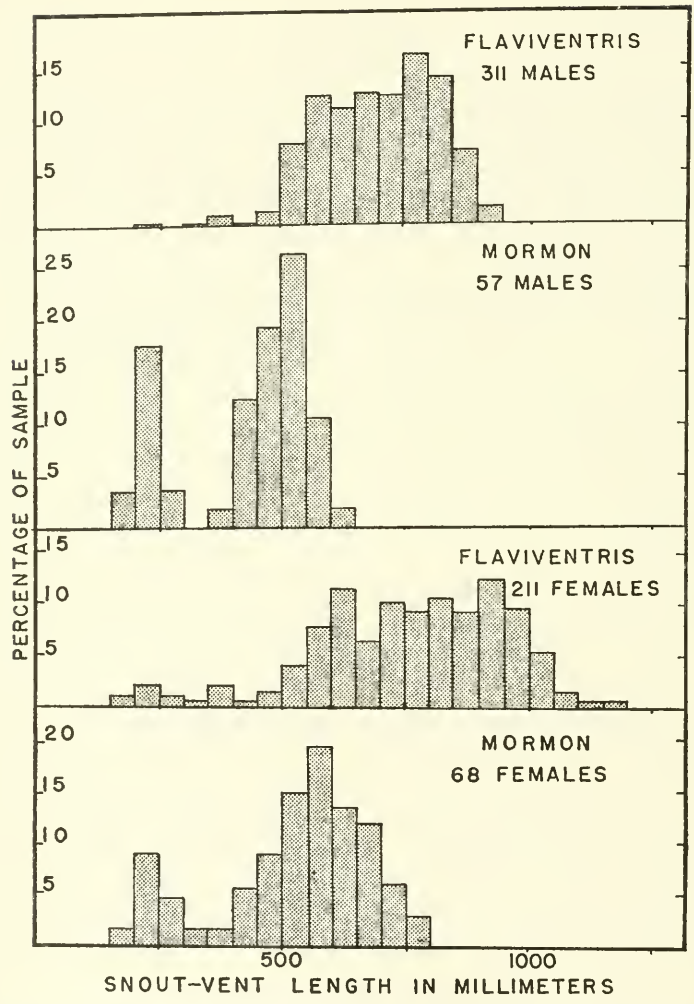


FIG. 20. Histograms comparing snout-vent length in random samples of *Coluber c. flaviventris* (those captured on the Reservation and Rockefeller Tract in 1960 and 1961) and *C. c. mormon* (specimens in the Museum of Vertebrate Zoology, University of California). In the museum sample, collected by conventional methods, the first-year young constitute a prominent and fairly distinct size group, whereas in the sample of racers from the Reservation and Rockefeller Tract, mostly caught in wire traps of quarter-inch mesh, relatively few young were secured. It is demonstrated that hatchlings are approximately the same length in both populations, but *flaviventris* grows much longer, and that the differences in length between the sexes is approximately the same in each population.

the fact that for the supposed two-, three- and four-year-olds combined, females comprise 51.2 per cent, but they comprise 55.6 per cent of those more than four years old and 61.3 per cent of those more than five years old.

By assigning to each racer caught an arbitrary age, on the basis of size according to Table 17, I calculated the population (exclusive of those snakes in their first year of life) to have the composition shown in Table 19.

TABLE 19. PERCENTAGES OF ADULT POPULATION OF BLUE RACERS COMPRISED BY EACH ANNUAL AGE GROUP

YEARS OF AGE	2	3	4	5	6	7	8	9	10	11 or more
Percentage of population...	41.5	17.8	12.6	9.5	6.1	4.3	2.7	2.4	1.2	1.9

Figures are completely lacking to show the relative numbers of juveniles, until, already approaching adult size, the young are about to enter their second hibernation. My combined fall samples include 303 of these latter young, as against 142 racers about to enter their third hibernation. Thus, after having nearly attained adult size, these adolescent snakes sustained a loss of 53 per cent in a year. Losses must occur at an even more rapid rate in the younger and smaller snakes. It may be speculated that of the approximately 300 eggs produced by a population of 100 adult racers, 150 are lost before or during the period of incubation which lasts nearly two months. Of the 150 hatchlings emerging in early September, at least one-third probably are eliminated by the following breeding season in late May, leaving 100. The 100 survivors at this stage are still small juveniles, but by autumn they have attained adolescent size. By this time, if they had undergone a further reduction by 53 per cent, only 47 would remain—approximately the number to be expected if the population were stable from year to year.

A notable difference between the fall sample and the spring sample that I obtained was the higher proportion of large and old racers in the former sample. This difference can be attributed to the year-to-year changes in the population during the 14 consecutive years spanned by my field work. The fall sample of 734 racers represented the combined catch of the years 1949 through 1962, rather evenly distributed, but the spring sample included few snakes from the years 1949 through 1957; most were from the years 1958

through 1961. In 1949 when the study was begun, the Reservation was being protected for the first time, and formerly overgrazed pastures or cultivated fields were acquiring a rank growth of grass and weedy vegetation, and thus becoming favorable habitat. The abundant new habitat promoted rapid increase in the population of racers until the newly available areas were filled to their "carrying capacity." Table 21 shows the changing trends of the different age groups. Although the separate annual samples are perhaps too small to show the composition of the population accurately, it is significant that in the fall of 1949 an unusually high proportion of the racers caught were one-year-olds, hatched in September, 1948.

Table 20 shows that in a typical group of 100 subadult and adult racers (second year and older) only a little more than one-fourth are productive females. The largest females, six years old and older, making up less than ten per cent of the adult population, contribute nearly half the total complement of eggs.

The calculated number of eggs pertains to a stage before oviposition, and subsequent losses through resorption under unfavorable conditions, through inviability of embryos and through deaths of some of the gravid females, are to be expected. In the weeks of incubation further losses are sustained. Although these losses cannot be measured, they must be severe as on numerous occasions scattered and torn eggshells representing entire clutches dug out and destroyed by predators, have been found. Probably other clutches are destroyed underground by such predators as moles and egg-eating snakes, and still others by insects. Tinkle (1959:195) wrote that in a clutch of 15 eggs found under a board, four were parasitized and had small perforations. Molds destroy a high percentage of all reptilian eggs that are incubated artificially and doubtless destroy many under natural conditions also. Excessive heat or moisture, or desiccation, resulting either from climatic extremes or from poor choice of a nest site by the female, would cause further loss. In four different years, Blair (1960:108) found that losses of eggs between laying and hatching in the Texas spiny lizard (*Sceloporus olivaceus*) ranged from 69 per cent to 86 per cent; no other comparable study of the extent of egg losses in a species of reptile is known to me. The racer is somewhat less prolific than the spiny lizard, and potentially longer lived; the racer's eggs are larger and thicker-shelled, and they are deposited in deeper burrows. It might be expected that losses during incubation would be somewhat less in the racer than in the spiny lizard.

Although figures for the youngest age groups—one-year-olds and hatchlings—are missing, approximations of them may be furnished by extrapolation, from the information available regarding the productivity of the population. Some factors involved in productivity are that the sex ratio deviates from parity, slightly in favor of the females in the adolescents but more markedly in favor of the females among the older age groups; that some adult females apparently fail to produce eggs in the breeding season, but the percentage decreases in the older snakes; and that number of eggs

TABLE 20. CALCULATED PRODUCTIVITY IN A HYPOTHETICAL GROUP OF 100 SUBADULT AND ADULT BLUE RACERS

AGE-GROUP (years)	Percentage of population in age-group	Percentage of fecund females in age-group	Percentage productive females in age-group	Eggs per productive female	Number of eggs produced
2	41.5	51.2	13	9.2	26
3	17.8	51.2	56	9.9	51
4	12.6	51.2	60	10.8	42
5	9.5	55.0	57	13.0	39
6 and over	18.6	61.3	80	15.7	143

TABLE 21. PERCENTAGES OF RACERS IN EACH ANNUAL AGE GROUP (EXCLUSIVE OF HATCHLINGS) IN AUTUMNAL SAMPLES AT DIFFERENT STAGES OF THE FIELD STUDY, SHOWING SHIFT TOWARD OLDER AGE-GROUPS IN THE LATER YEARS

	Year or combination of years represented by each sample				
YEARS OF AGE	1949	1950 1951 1952	1953 1954 1955	1956 1957 1958	1959 1960 1961 1962
1	54	44	39	39	41
2	14	24	21	19	19
3	18	11	23	16	13
4	4	10	10	11	9
5	6	6	3	8	8
6	2	1	3	1	3
7	2	4	4	2	3
8	.....	.....	.....	.5	2
9	.....	1	.4	.5	2
10	.....	.....	.4	2	1
Older than 10	.....	.....	.....	.5	.....
Number in sample	49	126	117	194	242

per clutch increases in proportion to the size and age of the female producing them. Too few figures are available concerning most of these factors to indicate more than the trends; nevertheless the available figures have been used in Table 20 in an attempt to estimate the productivity of a hypothetical population.

Numbers

Conant (1938:178, Pl. 7) published a photograph of 106 blue racers killed in February, 1932, by farmers near Bellville, Ohio, and Pope (1944:173) mentioned that scores of blue racers aggregated in October around an oak-covered dune near Chicago. In both these instances large hibernating aggregations were involved, and the areas represented by them are unknown; nothing has been recorded regarding population densities.

The records obtained through my fall trapping, along hilltop rock outcrops, yielded no information concerning population densities, but those obtained in fields in summer did provide significant information in this regard. Even after years of trapping on the same area, the catch still consisted largely of new individuals; the method was not sufficiently effective to catch all racers present at any one time, and the total catch for a season therefore provided only a crude index of the minimum number present.

The summer trapping was carried on in three separate areas. One of these was the area of bottomland pastures and formerly cultivated fields where the Reservation headquarters are located, a block of 39 acres bounded on three sides by woodland, and on the fourth by cultivated farm land. Effective trapping in this area was carried on through the years 1955 to 1961 inclusive. A second area, of 48 acres, was one of upland fields, mostly covered with reestablished prairie grasses, in the northeastern part of the Reservation. A third area, of 137 acres, also upland, was that of the Rockefeller Tract, cultivated through 1956 and sown to prairie grasses the following year, and the adjacent northwestern hilltop portion of the Reservation. Effective trapping on these two latter areas was carried on in 1958 through 1962.

For the seven years of trapping in the House Field area, the catch was as follows: 30, 33, 38, 38, 34, 24, and 20. In four years of trapping, the northeast field area yielded 42, 28, 37, 59, and 19 blue racers, and the Rockefeller Tract yielded 52, 67, 67, 126, and 106. The actual catch was hence less than one per acre in nearly all instances, but the year-to-year differences in catch are believed

to be caused chiefly by differences in numbers of traps used and in trapping effort, rather than by changes in the numbers of racers present.

Best index to the number of racers actually present is provided by the number of recaptures, and their ratio to first captures. The population of course, undergoes alteration from year to year, with many racers eliminated and replaced by others.

In 1955, 26 racers were caught in the May-June-July period, in the headquarters field area. In the August-September-October period of the same year five racers were caught of which only one was a member of the original 26. The five-to-one ratio indicates that the original 26 may have represented an actual population of 130, but of course the single recapture is much too small a sample to provide a reliable ratio. Some of the racers caught in May were recaptured in June, others in July, and still others not until late summer or early autumn. Somewhat different estimates can be obtained for the population depending on how the season's records are divided. For instance, in the headquarters field area in May 1955, eleven racers were caught; in the remainder of the season 20 were caught, of which two were members of the original group of eleven. The 20 to 2 ratio indicates that the 11 caught in May represented an actual population of 110. In the period May-June, 18 racers were caught, and in July-August-September-October, 15 were caught, including four of the original 18, hence indicating a population of 67. Although obviously the population underwent some change during the course of the season, the three sets of census figures apply essentially to the same population, and the divergence in them illustrates the wide range of error arising from insufficiently small samples.

Common sources of error in the censusing of natural populations of animals by the capture-recapture method ("Lincoln Index" or "Petersen Index") arise from the fact that the composition of a local population often changes between two sampling periods, or even within them. Some of the animals marked may move elsewhere, to be replaced by unmarked immigrants, or they may die and be replaced by unmarked maturing young. First-year racers that could pass through the quarter-inch mesh of the traps in spring and early summer became too large to escape in this way in the latter half of the summer, but these young were excluded from the census computations. There was doubtless some shifting of marked individuals away from the study areas and shifting of new individuals onto

these areas in the periods of weeks between successive samplings. Jackson (1939) has explained a method of correcting census computations based on capture-recapture ratios when there is a consistent trend of diminishing recaptures with increase in elapsed time. However, in my records no such trend is discernible; furthermore it has been demonstrated that individual racers tend to stay within the same home range area throughout most of their season of activity. Therefore, I conclude that shifts of individuals away from the study areas or into them, in the intervals between samplings constitute only a minor source of error.

A combination of the figures from the three samples listed above provides an intermediate "smoothed" figure that can be accepted with somewhat more confidence than any one of the separate censuses because it is based on more records. The combined ratios indicate a total of 105 racers in the headquarters field area. The figures obtained in the different sampling periods, and the census figures derived from their ratios are shown in tables 22 and 23. Differences from year-to-year in the census figures for any one area show no consistent trends and their variation is similar to that shown in different samples for the same season. Probably populations were fairly stable throughout the periods involved. If such stability is assumed, the samples from different years may be combined, and the composite figures derived from them may be accepted with more confidence. For the headquarters field area, for instance, 419 records of racers were gathered in all the preliminary sampling periods of the seven seasons involved; the records totalled 263 for all the secondary sampling periods, with 70 recaptures in secondary periods of the snakes recorded in the corresponding preliminary periods. A population of 75 racers is indicated—1.9 per acre. Corresponding figures for the northeast field area are: preliminary samples 453, secondary samples 163, recaptures 39, calculated number 135 (2.82 per acre). For the Rockefeller Tract the figures are as follows: Preliminary samples 807, secondary samples 476, recaptures 126, the ratio indicating a population of 153, or 1.11 per acre.

These figures represent the number of adults present in early summer when the population is near its annual low point. The first-year young, excluded from this census because they cannot be caught in representative numbers, perhaps approximate the number of adults, in May, so the figures obtained would need to be approximately doubled to be representative of the entire population.

By late summer the adults, and especially the yearlings, have undergone substantial reduction in numbers, but in late August and early September the hatching of a new crop of young increases the population to its annual maximum. The maximum numbers probably are about three times those obtained by censusing adults in early summer. The peak population of late summer or early autumn is estimated to consist of hatchlings, comprising somewhere near 50 per cent; adults, comprising a little more than 25 per cent; and yearlings comprising a little less than 25 per cent.

Densities in early summer of one to three adult blue racers per

TABLE 22. CAPTURES RECORDED AND POPULATION CALCULATED FROM THEM ON HILLTOP GRASSLAND AREAS OF ROCKEFELLER EXPERIMENTAL TRACT AND ADJACENT RESERVATION IN FOUR DIFFERENT YEARS

	1959	1960	1961	1962	Four-year average
First Census:					
Early May	0	8	21	32	61
Late May	3	13	33	35	84
Recaptures	0	1	2	7	10
Estimated population	.....	104	346	160	128
Second Census:					
May	3	25	54	59	141
June	9	6	25	40	80
Recaptures	0	3	6	24	33
Estimated population	.....	50	165	99	85
Third Census:					
May-June-July	25	34	94	100	253
Sept.-Oct.	8	13	20	13	54
Recaptures	1	3	5	4	13
Estimated population	200	182	376	324	263
Fourth Census:					
May-June	31	30	73	76	210
July-Aug.-Sept.-Oct.	24	15	34	35	108
Recaptures	3	2	14	12	31
Estimated population	104	225	177	222	183
Fifth Census:					
May	3	25	54	60	142
June to October	23	20	67	40	150
Recaptures	0	5	14	20	39
Estimated population	.....	100	258	120	162
Five Sets Combined:					
Combined first samples	62	122	296	327	807
Combined second samples	67	67	179	163	476
Recaptures	4	14	41	67	126
Estimated population	208	117	258	159	153

acre probably are typical of the better types of habitat in the region of my study. The upland field area estimated to have 2.82 racers per acre was better habitat than the other two study areas. Prior to 1948 it had been cultivated and severely eroded. In 1949 most of it was sown to seeds of prairie grasses, and by 1958 different parts of it were dominated by different species of native perennial tall grasses interspersed with areas that supported a weedy type of vegetation, and other areas that supported dense thickets of sumac, dogwood, elm saplings, or other woody plants. The abundance and diversity of dense cover and of small animals made this area especially favorable habitat for the racer.

Some local areas probably support higher populations of racers

TABLE 23. CAPTURES RECORDED AND POPULATIONS ESTIMATED FROM THEM IN HEADQUARTERS FIELD AREA OF RESERVATION

	1955	1956	1957	1958	1959	1960	1961	Seven-year average
First Census:								
May	11	21	7	24	17	13	6	99
June-July-Aug.	20	11	25	20	22	12	14	124
Recaptures	2	1	4	5	5	2	0	19
Estimated population	110	231	44	96	75	78	.....	92
Second Census:								
May-June	18	25	17	28	27	15	13	143
July-Aug.-Sept.-Oct.	15	8	17	15	15	11	8	89
Recaptures	4	1	7	5	9	3	1	30
Estimated population	68	200	41	84	45	55	104	61
Third Census:								
May-June-July	26	28	22	31	31	20	19	177
Aug.-Sept.-Oct.	5	7	13	12	6	5	2	50
Recaptures	1	2	7	5	3	1	1	20
Estimated population	130	128	47	87	63	75	148	63
Three Sets Combined:								
Combined first samples	55	74	46	83	75	48	38	419
Combined second samples	40	26	55	47	43	28	24	263
Combined recaptures	7	4	18	15	17	6	3	70
Estimated population	105	160	47	87	63	75	101	75

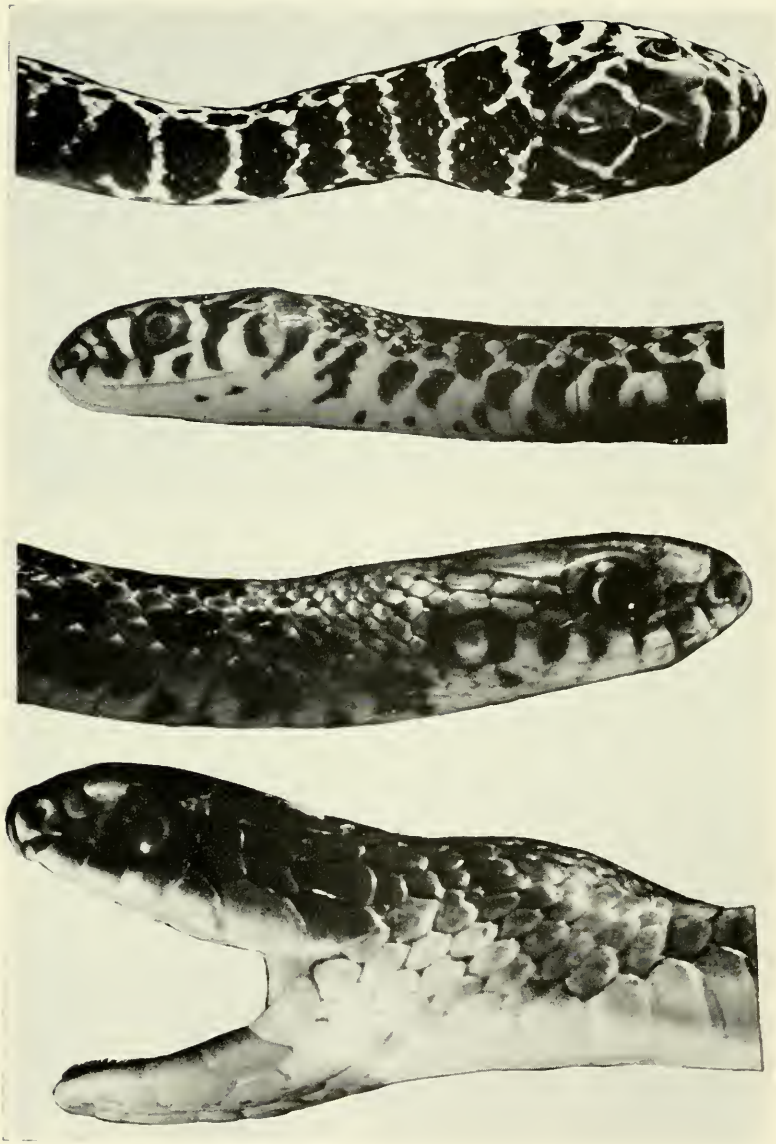


FIG. 1. Head of hatchling blue racer, dorsal view, September 1962, approximately × 3.

FIG. 2. Head of hatchling blue racer, lateral view, September 1962, approximately × 3.

FIG. 3. Head of yearling male blue racer, lateral view, August 1, 1961, a little less than twice natural size.

FIG. 4. Head of adult male blue racer, lateral view, July 16, 1961, approximately × 2. All three snakes from Rockefeller Experimental Tract, Jefferson County, Kansas.

FIG. 1. Abandoned limestone quarry on a hilltop of southward exposure on The University of Kansas Natural History Reservation, in late autumn of 1931. The crevices along the base of the ledge provided favorite hibernating sites for blue racers.

FIG. 2. Hatchling blue racer and eggshell from which it had recently emerged, in early September, 1962; × approximately $1\frac{2}{3}$.

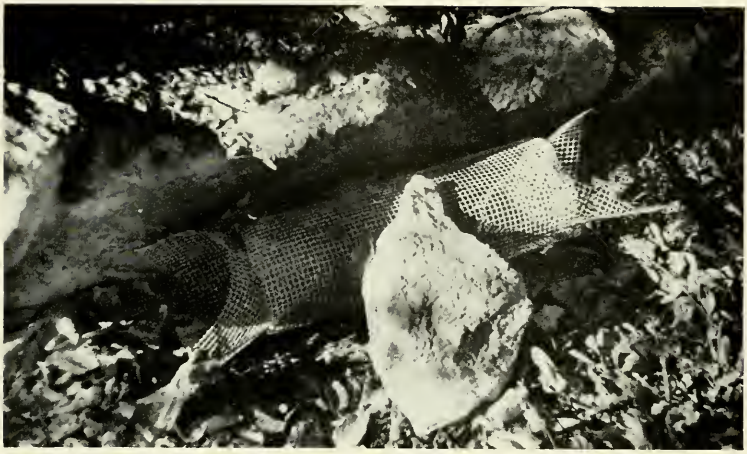


FIG. 1. Wire funnel trap set at base of hilltop limestone outcrop in a spot strategically located for interception of blue racers searching for deep crevices in which to hibernate, October 15, 1949.

FIG. 2. Large clutch of 21 blue racer eggs, recently plowed out, at Harold Brune farm, Jefferson County, Kansas, July 10, 1962.

FIG. 1. Habitat of blue racer, bluestem prairie on Botany Bluff at northwest corner of the University of Kansas Natural History Reservation, looking south. Trees and brush in background are along limestone outcrop at top of slope. Mowed area in foreground is southwest corner of Rockefeller Experimental Tract, a privately owned farm at the time this photograph was taken in the summer of 1951.

FIG. 2. Habitat of blue racer, bluestem prairie on south slope of Botany Bluff, looking north along west edge of the Reservation, summer of 1951. By 1962, with exclusion of fire, and protection from mowing, prairie vegetation had largely disappeared from this slope, and had been replaced by trees and brush. As a result of these successional changes racers no longer found this slope a suitable habitat in summer, but they continued to resort to the hilltop rock outcrop to hibernate in autumn.

than do areas where censuses were made, but under modern conditions, situations that offer near optimum habitat are not likely to be extensive or to persist long. On land that is capable of producing a good crop of vegetation, the crop is usually harvested either by grazing of livestock or by using the land for cultivation, with the result that the racers are, at least in some seasons, forced into marginal situations. More than 50 years ago in Missouri, Hurter (1911:170) wrote that the racer "was quite common 20 years ago in pastures, meadows and fields but as cultivation has advanced it is becoming quite rare." In 1962 the widespread and adaptable blue racer is still common in many parts of its range, including Missouri, but in most places its population densities probably are lower than formerly.

Reduction since 1911 has probably been far more drastic than the reduction that had occurred up to that time. Schmidt and Necker (1935:69), writing of the racer in the Chicago region, noted "the snakes which raise their heads and face mowing machinery tend to be exterminated in agricultural areas." They stated that in the Chicago region the racer had been exterminated by the advance of agriculture except in two extensive sand dune areas. In July 1962, Mr. V. B. Howell, a progressive farmer of the Great Bend area in central Kansas, told me that the kinds of snakes inhabiting cultivated land—blue racer, bull snakes, prairie king snakes, hognosed snakes, and others—had undergone great reduction in numbers during the period of his farming. He estimated that in a forty-year period the numbers had declined to perhaps five per cent of their level in the area most familiar to him, centering at his farm 11 miles northwest of Great Bend, Barton County. In accounting for this change in population density Howell pointed out the relative destructiveness to small animals of modern farm machinery as contrasted with horse-drawn equipment or that used with tractors of earlier models. Modern tractors move forward so rapidly that there is little opportunity for snakes or other small animals to avoid them, and the plows and disks cut wide swaths penetrating more deeply into the soil than did older types. On July 10, 1962, in searching the furrows of a freshly plowed small field on the Harold Brune farm, for turned-up nests of the snakes, I found two adult blue racers that had been struck and killed by the plow, possibly while they were underground. In fields that are plowed or cultivated between the times of egg-laying and hatching, the eggs are destroyed. Because of its rapid movements and alertness, the racer

is more likely to escape farm machines than are most other kinds of snakes. Nevertheless, it is vulnerable and survives in cultivated areas only when they are interspersed with pastures, woodlots, or streamside thickets where at least part of the population may find refuge.

Summary

Field study of the blue racer was carried on in several localities in Kansas, but chiefly at the University of Kansas Natural History Reservation (the northeasternmost section of land in Douglas County), and the adjacent 160-acre Rockefeller Experimental Tract in Jefferson County. By October 26, 1962, after 14 years of field work, a total of 1423 racers had been captured some 2197 times.

The locale of the present study was near the geographic center of the blue racer's range. The range, chiefly in the Mississippi Valley and Great Plains region, is centrally situated with respect to the other seven subspecies. An extensive but scattered literature concerning the ecology of the species as a whole, and its several geographic races, has been reviewed and utilized for comparison with my own field data.

Blue racers were caught in wire funnel traps set in prairie and pastureland habitat in summer, and along hilltop limestone outcrops in woodland in autumn. The autumn trapping along rock outcrops was carried on each year from 1949 to 1962, but effective summer trapping was carried on only in the last six years of the study. Each racer caught was individually and permanently marked by scale clipping. More than half were caught only once, but many were recorded repeatedly, with a maximum of 16 captures.

The racer occurs throughout most of the United States, and its populations are subject to much geographic variation. The snakes are largest in the northeastern part of the range, with clines of decreasing size toward the southeastern, southern and western parts of the United States. There are somewhat parallel trends in coloration; the black racer of the northeastern states grades into paler, gray or light brown subspecies in southern Florida, Texas, and the far western states. Accompanying these changes in color and size are minor morphological changes and major ecological changes. The black racers of the eastern states often inhabit forest or forest-edge habitats while the paler and smaller snakes of more southern or western areas typically inhabit scrub, chaparral, or prairie. The large, dark-colored racers of the eastern and northeastern states are especially inclined to attack larger prey including small verte-

brates, even weasels, rabbits, and chipmunks, whereas the smaller and paler racers of more southern and more western areas take a higher proportion of insects and rarely attack vertebrates other than small reptiles.

On the area where field work was carried on in northeastern Kansas, tall-grass prairie habitat is preferred, but fields of grain or alfalfa, grazed pasture, brush, woodland edge, groves or open woodland, and weedy fields are all utilized to some extent. The racer is strictly diurnal and largely terrestrial but it may climb through bushes or small trees in foraging or escaping.

The blue racer is a typical colubrine snake of slender build, with large eyes, and vision plays an important role in finding prey and detecting enemies. In the adult blue racer the dorsal color is variable, pale brown or gray, bluish, greenish or slaty. In the hatchling, however, there is a distinct pattern of a type widespread among colubrines and also among snakes of other groups—a series of middorsal blotches on an olive ground color, with alternating rows of smaller spots on each side. The ventral surface is pale, with dark speckling. The pattern is sharply defined on the anterior part of the body, but markings become progressively more obscure posteriorly and are scarcely discernible on the tail.

The juvenal pattern fades gradually as growth proceeds, and there is much individual variation in the rate of its loss. Some racers still retain the juvenal pattern faintly discernible after attainment of sexual maturity. There are also striking ontogenetic changes in the proportions of the head, body and tail. The diameter of the eye is approximately one per cent of the snout-vent length in hatchlings, but is only a little more than half that relative size in the largest adults. In the course of allometric growth other parts of the head also enlarge less rapidly than the body, but more rapidly than the eye. In hatchlings there is a slight average difference between the sexes in relative tail length, with males' tails the longer. Relative tail length increases slightly in both sexes up to the time of sexual maturity, and then decreases slightly with advancing age.

Racers in northeastern Kansas spend nearly half the year in hibernation, with average recorded emergence date April 16, and average date of retirement into hibernation November 8. Hibernacula are usually in crevices in hilltop limestone outcrops with south exposures. Winter temperatures within the hibernacula are usually well within the range 0 degrees to 10 degrees Centigrade. Spring

emergence has been recorded at an air temperature of only 12.5 degrees Centigrade. Racers bask in sunshine frequently even in warm weather, and the temperature preferendum is several degrees higher than in most other kinds of snakes. Bodily temperatures obtained from blue racers that were fully active, either under natural conditions or in a large outdoor enclosure, were concentrated in the neighborhood of 34 and 35 degrees Centigrade. For short periods racers can survive temperatures up to 45 degrees without damage, but more prolonged exposure to temperatures of slightly less than 40 degrees can be fatal. In hibernation, racers can withstand temperatures slightly below freezing, but they cannot survive being frozen solid.

Blue racers tend to limit their activities to familiar areas or home ranges; some individuals may live out their entire lives within the same home range, but others shift from time to time. Average home ranges of approximately 26 acres for males and 24 acres for females were calculated. The racers' preference for hibernacula in a habitat different from that to which summer activities are confined necessitates spring and fall migrations between the limestone outcrops where hibernation occurs and the grasslands where the snakes stay in summer. The average spring or fall migration is approximately a quarter of a mile, but an individual racer does not consistently return to the same hibernaculum. Many racers were recorded to have made movements of 2000 to nearly 4000 feet, involving shifts in home range, but some later shifted back to their original areas. Some may have made even longer shifts but their movements would not have been recorded since they would have gotten beyond the limits of the study area.

Blue racers hunt by various methods, often by coursing through dense vegetation in active search in which vision is of primary importance in locating the prey. Almost any small animal that moves nearby may be overtaken and caught with a sudden dash. From analysis of scats and prey from stomachs, a total of 1357 food items of more than 50 species was compiled. Favorite prey species were the cricket (*Gryllus assimilis*), grasshoppers (*Arphia simplex, Melanoplus femur-rubrum, M. bivittatus, M. differentialis*), camel crickets (*Ceuthophilus* sp.), katydid (*Neoconocephalus robustus*), vole (*Microtus ochrogaster*), white-footed mouse (*Peromyscus* sp.), racerunner, (*Cnemidophorus sexlineatus*), and leopard frog (*Rana pipiens*). The insects taken greatly outnumbered the vertebrates, but the vertebrates made up most of the actual bulk of prey eaten.

Crickets, grasshoppers, and katydids comprised most of the insect prey. Beetles, moths and cicadas were rarely taken. Vertebrate prey included miscellaneous small snakes (some of them juvenal racers), mammals, and birds. Seasonal change in the composition of the food is slight, but vertebrates figure more prominently in early summer, and insects comprise increasing percentages later in the season. Composition of the food differs according to size of the snake; gryllid and ceuthophilid crickets are best represented in the food of juveniles whereas small mammals, and grasshoppers of the genus *Melanoplus* are best represented in the food of large adults.

The breeding season is mainly in May. Mating is promiscuous and two or more males may court the same female simultaneously. A courting male lies on or alongside a receptive female, with spasmodic rippling abdominal movements, and with his vent addressed to hers. At intervals in the courtship period the female moves swiftly for a few feet or a few yards shifting to a new spot, and during her activity the male strives to maintain contact with her. From time to time the male leaves the female briefly and courses rapidly around her in a devious route. Courtship is consummated when the female raises her tail in acceptance of the male and intromission is effected. During coitus, which lasts for periods of minutes, the female moves forward slowly, dragging the passive male, tail-first behind her.

Ovulation normally is in late May. Eggs from 29 to 39 millimeters in length and 14 to 21 millimeters in breadth are laid, from mid-June to early August, usually in tunnels of fossorial mammals such as voles or moles, at depths of five to 12 inches. Clutches of the blue racer average 11.8 eggs but the number is correlated with age and size of females; two-year-olds average only 9.2 eggs, whereas those females that are six years old or more average 15.7 eggs. Also, there is geographic variation in size of clutch, from only 5.8 eggs in *C. c. mormon* of the West Coast to 16.8 eggs in *C. c. constrictor* of the northeastern states. In each breeding season some females of adult size do not produce clutches. Only about 13 per cent of the two-year-olds in a small sample were fecund, but the ratio increased to 80 per cent in old adults. Incubation averages 51 (43 to 63) days.

Hatchlings usually make several longitudinal slits in the eggshell with the egg tooth before emerging, and often require a day or more to emerge after the first slit is made. Hatchlings average

10¾ inches and 4.16 grams. By late October when these young are ready to enter hibernation, they have grown to 16¾ inches and 12.3 grams. Typical October lengths (overall) in inches for males and females, respectively, after successive seasons of growth, are as follows: yearlings, 27¾ and 29; two-year-olds, 34¼ and 37¼; three-year-olds, 37¾ and 41¾; four-year-olds, 40 and 44¾; five-year-olds, 41½ and 46¼; six-year-olds, 42¼ and 48¼; seven-year-olds, 43¾ and 50; eight-year-olds, 44 and 51¼.

Judging from trends in the small samples available, sex ratio in hatchlings is approximately 1 : 1. In the summer trapping of blue racers, males are caught in larger numbers than females, but seemingly this is because of their greater activity. In fall along the limestone outcrops where the racers hibernate females were caught in slightly greater numbers than males among the young adults, and made up a little more than 60 per cent of the old adults. Presumably the males are eliminated more rapidly, because of their greater activity, their smaller size, or a combination of both factors. The composition by age groups of the adult racers captured was as follows: two-year-olds, 41.5 per cent; three-year-olds, 17.8 per cent; four-year-olds, 12.6 per cent; five-year-olds, 9.5 per cent; six-years-olds, 6.1 per cent; seven-year-olds, 4.3 per cent; eight-year-olds, 2.7 per cent; nine-year-olds, 2.4 per cent; ten-year-olds, 1.2 per cent; more than ten years old, 1.9 per cent.

Attempts to census blue racers on the study plots, from the capture-recapture ratios, yielded highly variable figures for different areas and even for the same area at different times. Variability is believed to result mostly from the small sizes of the samples, none of which is large enough to yield a census figure that is statistically reliable. Combined samples yielded figures indicating populations of one to three adults per acre in early summer in areas of favorable habitat. To represent the entire population in late summer—the time of its annual maximum—these figures would need to be approximately tripled.

The blue racer depends mostly on speed to escape its enemies. In escaping it often takes advantage of a downhill slope to increase its speed. A racer startled at close range often sets out with a violent thrashing that attracts attention to a given spot, then glides away so silently and rapidly that its course is not detected. The snake may circle back and approach the scene of disturbance slowly and stealthily, from the direction opposite to that taken in departing. Often a racer seeks concealment by climbing into a bush or

tree, and occasionally escape is effected by swimming. A racer that is caught or cornered usually makes a spirited defense by striking and biting. An alternative reaction, seen most typically when the snake is handicapped by injury or by low temperature, is to coil with the head concealed, and, with writhing movements, to smear the surface of the body with musk discharged from glands in the base of the tail.

Many natural enemies prey upon the racer, but in the present study the majority of records pertained to the red-tailed hawk. The broad-winged hawk, marsh hawk, red-shouldered hawk, sparrow hawk, and barn owl also are among the raptors that feed on this kind of snake. Among mammals the striped skunk is the only species definitely recorded to prey on the racer, feeding on the eggs as well as upon the young and adults. The common king snake, prairie king snake, timber rattlesnake, copperhead, and even the slender glass lizard have been recorded to prey on the blue racer, but probably all are of minor importance as natural enemies. Shrews (*Blarina, Cryptotis*) and mice (*Peromyscus, Reithrodontomys*) have sometimes killed and eaten racers confined in traps, and under natural conditions they possibly prey upon snakes that are immobilized when torpid from cold, in their hibernacula and temporary shelters. Chiggers are the most common ectoparasites of the racers. Four species of the chigger genus *Trombicula* have been recorded on racers from the Reservation. The racer is an important host of the common pest chigger, *Trombicula alfreddugèsi,* which often attacks humans. Most adult racers on the Reservation and nearby areas carry the fluke, *Neorenifer lateriporus.* In spring these flukes are conspicuous in the mouths of the racers, but in late summer they are not in evidence.

Literature Cited

ALLEN, M. J.
1932. A survey of the amphibians and reptiles of Harrison County, Mississippi. Amer. Mus. Novit., 542:11-12.

ANDERSON, P.
1942. Amphibians and reptiles of Jackson County, Missouri. Bull. Chicago Acad. Sci., 6:203-220.

ATKINSON, D. A.
1951. The reptiles of Allegheny County, Pa. Ann. Carnegie Mus., 1:145-157.

AUFFENBERG, W.
1949. The racer, *Coluber constrictor stejnegerianus* in Texas. Herpetologica, 5:53-58.
1955. A reconsideration of the racer, Coluber constrictor, in eastern United States. Tulane Studies in Zool., 2(6):89-155.

BARBOUR, R. W.
1950. The reptiles of Big Black Mountain, Harlan County, Kentucky. Copeia, 1950:100-107.

BAXTER, G. T.
1947. The amphibians and reptiles of Wyoming. Wyoming Wild Life, August and October 1947:1-8.

BLAIR, W. F.
1960. The rusty lizard. Univ. Texas Press, Austin, xvi + 185 pp.

BLANCHARD, F. N. and BLANCHARD, F. C.
1942. Mating of the garter snake, *Thamnophis sirtalis sirtalis* (Linnaeus). Papers Michigan Acad. Sci. Arts and Letters, 27:215-234.

BLANCHARD, F. N. and FINSTER, E. B.
1933. A method of marking living snakes for future recognition with a discussion of some problems and results. Ecology, 14:334-349.

BOGERT, C. M. and COWLES, R. B.
1947. Moisture loss in relation to habitat selection in some Floridian reptiles. Results of the Archbold Expeditions, No. 58; Amer. Mus. Novit., 1358:1-34.

BONN, E. W. and MCCARLEY, W. H.
1953. The amphibians and reptiles of the Lake Texoma area. Texas Jour. Sci., 1953(4):465-471.

BOYER, D. A. and HEINZE, A. A.
1934. An annotated list of the amphibians and reptiles of Jefferson County, Missouri. Trans. Acad. Sci. St. Louis, 28(4):183-200.

BRANSON, E. B.
1904. Snakes of Kansas. Univ. Kansas Sci. Bull., 12(13):353-430.

BRATTSTROM, B. H.
1953a. Records of Pleistocene reptiles and amphibians from Florida. Quart. Jour. Florida Acad. Sci., 16(4):243-248.

1953b. The amphibians and reptiles from Rancho La Brea. Trans. San Diego Soc. Nat. Hist., 11(14):365-392.

1955. Pliocene and Pleistocene amphibians and reptiles from southeastern Arizona. Jour. Paleontology, 29(1):150-154.

BRECKENRIDGE, W. J.
1944. Reptiles and amphibians of Minnesota. Univ. Minnesota Press, 202 pp.

BRIMLEY, C. M.
1903. Notes on the reproduction of certain reptiles. Amer. Nat., 37: 261-266.

BRONS, H. A.
1882. Notes on the habits of some western snakes. Amer. Nat., 16:564-567.

BRUMWELL, M. J.
1951. An ecological survey of the Fort Leavenworth Military Reservation. Amer. Midl. Nat., 45(1):187-231.

BURT, C. E.
1927. An annotated list of the amphibians and reptiles of Riley County, Kansas. Occas. Papers Mus. Zool. Univ. Michigan, 189:1-9.

1933. Some distributional and ecological records of Kansas reptiles. Trans. Kansas Acad. Sci., 36:186-208.

1935. Further records of the ecology and distribution of amphibians and reptiles in the Middle West. Amer. Midl. Nat., 16(3):311-336.

BURT, C. E. and HOYLE, W. L.
1934. Additional records of the reptiles of the central prairie region of the United States. Trans. Kansas Acad. Sci., 37:193-216.

CAGLE, F. R.
1942. Herpetological fauna of Jackson and Union counties, Illinois. Amer. Midl. Nat., 28(1):164-200.

CARPENTER, C. C.
1958. Reproduction, young, eggs and food of Oklahoma snakes. Herpetologica, 14:113-115.

CARR, A. F. JR.
1940. A contribution to the herpetology of Florida. Univ. Florida Publ. Biol. series, 3:iv + 118 pp.

CLARK, R. F.
1949. Snakes of the hill parishes of Louisiana. Jour. Tennessee Acad. Sci., 24(4):244-261.

CLARKE, R. F.
1958. An ecological study of reptiles and amphibians of Osage County, Kansas. Emporia State Research Studies, 7(1):1-52.

COHEN, E.
1948. Emergence of *Coluber c. constrictor* from hibernation. Copeia, 1948:137-138.

Committee on Herpetological Common Names
1956. Common names for North American amphibians and reptiles. Copeia, 1956(3):172-185.

CONANT, R.
1938. The reptiles of Ohio. Amer. Midl. Nat., 20(1):1-200.
1958. A field guide to reptiles and amphibians of the United States and Canada east of the 100th Meridian. Houghton-Mifflin Co., Boston xviii + 366 pp., 40 pls., 62 figs., 248 maps.

COPE, E. D.
1900. The crocodilians, lizards and snakes of North America. Rept. U. S. Nat. Mus. for 1898, pp. 153-1270.

CRABB, W. D.
1941. Food habits of the prairie spotted skunk in southeastern Iowa. Jour. Mamm., 22(4):349-364.

CROW, H. E.
1913. Some trematodes of Kansas snakes. Univ. Kansas Sci. Bull., 7:123-134.

CUNNINGHAM, J. D.
1959. Reproduction and food of some California snakes. Herpetologica, 15(1):17-19.

CURTIS, L.
1949. The snakes of Dallas County, Texas. Field & Laboratory, 17:5-13.

DICE, L. R.
1916. Distribution of the land vertebrates of southeastern Washington. Univ. California Publ. Zool., 16(17):293-348.

DITMARS, R. L.
1896. The snakes found within fifty miles of New York City. Abs. Proc. Linn. Soc. New York, 8:9-24.
1907. The reptile book. Doubleday, Page and Co., New York, pp. xx + 472.
1944. Serpents of the northeastern states. New York Zool. Soc., 34 pp., 21 pls.

DUELLMAN, W. E.
1951. Notes on the amphibians and reptiles of Greene County, Ohio. Ohio Jour. Sci., 51(6):335-341.

DUELLMAN, W. E. and SCHWARTZ, A.
1958. Amphibians and reptiles of southern Florida. Bull. Florida State Mus. Biol. Sci., 3(5):181-324.

Ellicott, E. L.
1880. Bundles of snakes. Am. Nat., 14:206-207.

Etheridge, R. E.
1952. The southern range of the racer *Coluber constrictor stejnegerianus* (Cope), with remarks on the Guatemalan species *Coluber ortenburgeri* Stuart. Copeia, 1952:189-191.

Ferguson, D. E.
1952. The distribution of amphibians and reptiles of Wallowa County, Oregon. Herpetologica, 8:66-68.

Finneran, L. C.
1948. Reptiles at Branford, Connecticut. Herpetologica, 4:123-126.

Fitch, H. S.
1935. Natural history of the alligator lizards. Trans. Acad. Sci. St. Louis, 29(1):1-38.

1936. Amphibians and reptiles of the Rogue River Basin, Oregon. Amer. Midl. Nat., 17(3):634-652.

1940. A biogeographical study of the ordinoides artenkreis of garter snakes (genus Thamnophis). Univ. California Publ. Zool., 44(1): 1-150.

1949. Road counts of snakes in western Louisiana. Herpetologica, 5: 87-90.

1951. A simplified type of funnel trap for reptiles. Herpetologica, 7: 77-80.

1954. Life history and ecology of the five-lined skink, *Eumeces fasciatus*. Univ. Kansas Publ. Mus. Nat. Hist., 8(1):1-156.

1955. Habits and adaptations of the Great Plains skink. Ecol. Monogr., 25(3):59-83.

1956. Temperature responses in free-living amphibians and reptiles of northeastern Kansas. Univ. Kansas Publ. Mus. Nat. Hist., 8(7): 417-476.

1958. Home ranges, territories and seasonal movements in vertebrates of the Natural History Reservation. Univ. Kansas Publ. Mus. Nat. Hist. 11(3):63-326.

1960. Autecology of the copperhead. Univ. Kansas Publ. Mus. Nat. Hist., 13(4):85-288.

Fitch, H. S. and Packard, R. L.
1955. The coyote on a natural area in northeastern Kansas. Trans. Kansas Acad. Sci., 58:211-221.

Fitch, H. S. and Sandidge, L. L.
1953. Ecology of the opossum on a natural area in northeastern Kansas. Univ. Kansas Publ. Mus. Nat. Hist., 7(2):305-338.

Force, E. R.
1930. The amphibians and reptiles of Tulsa County, Oklahoma, and vicinity. Copeia, 1930(2):25-39.

Fouquette, M. J. and Lindsay, H. L., Jr.
1955. An ecological survey of reptiles in parts of northwestern Texas. The Texas Jour. Sci., 7(4):402-421.

Gloyd, H. K.
1928. The amphibians and reptiles of Franklin County, Kansas. Trans. Kansas Acad. Sci., 31:115-141.

1932. The herpetological fauna of the Pigeon Lake region, Miami County, Kansas. Papers Michigan Acad. Sci. Arts and Letters, 15:389-409.

1945. The problem of too many snakes. Chicago Nat., 7(4):87-97.

Grinnell, J., Dixon, J., and Linsdale, J. M.
1930. Vertebrate natural history of a section of northern California through the Lassen Peak region. Univ. Calif. Publ. Zool., 35: v + 594 pp., 181 figs.

GUIDRY, E. V.
1953. Herpetological notes from southeastern Texas. Herpetologica, 9:49-56.

HAMILTON, W. J., JR., and POLLACK, J. A.
1956. The food of some colubrid snakes from Fort Benning, Georgia. Ecology, 37:519-526.

HARWOOD, P. D.
1933. The helminths parasitic in the Amphibia and Reptilia of Houston, Texas and vicinity. Proc. U. S. Nat. Mus., 81, 17:1-71.

HAY, O. P.
1893. On the breeding habits, eggs, and young of certain snakes. Proc. U. S. Nat. Mus., 15:385-397.

HIBBARD, C. W.
1936. The amphibians and reptiles of Mammoth Cave National Park Proposed. Trans. Kansas Acad. Sci., 39:277-281.

HUDSON, G. E.
1942. The amphibians and reptiles of Nebraska. Nebraska Conservation Bull. no. 24, 146 pp.

HUDSON, R. G.
1949. A record length milk snake. Herpetologica, 5:47.

HURTER, J. H.
1911. Herpetology of Missouri. Trans. Acad. Sci. St. Louis, 20:59-274.

INGER, F. and CLARK, P. J.
1943. Partition of the genus *Coluber*. Copeia, 1943(3):141-145.

JACKSON, C. H. N.
1939. The analysis of an animal population. Jour. An. Ecology, 8:238-246.

KING, W.
1939. A survey of the herpetology of Great Smoky Mountain National Park. Amer. Midl. Nat., 21(3):531-582.

KLIMSTRA, W. D.
1959. Food of the racer, *Coluber constrictor*, in southern Illinois. Copeia, 1959(3):210-214.

LANGBARTEL, D. A.
1947. Snakes collected at Camp Eastman, Hancock County, Illinois. Herpetologica, 4:27-28.

LINER, E. A.
1949. Notes on the young of the blue racer, *Coluber constrictor flaviventris*. Copeia, 1949(3):230.
1954. The herpetofauna of Lafayette, Terrebonne, and Vermilion parishes, Louisiana. Proc. Louisiana Acad. Sci., 17:65-85.
1955. A herpetological consideration of the Bayou Tortue region of Lafayette Parish, Louisiana. Proc. Louisiana Acad. Sci. 18:39-42.

LINSDALE, J. M.
1927. Amphibians and reptiles of Doniphan County, Kansas. Copeia, no. 164:75-81.

LOEWEN, S. I.
1940. On some reptilian cestodes of the genus Oochoristica (Anoplocephalidae). Trans. Amer. Microscop. Soc., 59(4):511-518.

LOGIER, E. B. S.
1932. Some account of the amphibians and reptiles of British Columbia. Contr. Royal Ontario Mus., Trans. Royal Canadian Inst., 18(2): 311-336.

LOOMIS, R. B.
1956. The chigger mites of Kansas (Acarina, Trombiculidae). Univ. Kansas Sci. Bull., 37, pt. 2(19):1195-1443.

LORD, J. K.
1866. The naturalist in Vancouver Island and British Columbia. Richard Bentley, London, 375 pp.

Marr, J. C.
1944. Notes on amphibians and reptiles from the central United States. Amer. Midl. Nat., 32:478-490.

Martin, E. P.
1956. A population study of the prairie vole (*Microtus ochrogaster*) in northeastern Kansas. Univ. Kansas Publ. Mus. Nat. Hist., 8(6): 361-416.

Maslin, T. P.
1959. An annotated check list of the amphibians and reptiles of Colorado. Univ. Colorado Studies, Biol. Series, No. 6, 98 pp.

McCauley, R. H.
1945. The reptiles of Maryland and the District of Columbia. Published by the author, Hagerstown, Maryland, 194 pp.

Minton, S., Jr.
1944. Introduction to the study of reptiles in Indiana. Amer. Midl. Nat., 32:438-477.

1949. An ectopic egg in Coluber. Herpetologica, 5:96.

Mossiman, J. E. and Rabb, G. B.
1952. The herpetology of the Tiber River area, Montana. Copeia, 1952(1):23-27.

Mulaik, S. and Mulaik, D.
1942. A neglected species of Coluber. Copeia, 1942:13-15.

Munro, D. F.
1948. Comparative sizes of two female blue racers and their eggs. Herpetologica, 4:199-200.

1949. Eating habits of young *Coluber constrictor flaviventris*. Herpetologica, 5:72-73.

1950a. Incubation and hatching of eggs of *Coluber c. flaviventris*. Herpetologica, 6:122-124.

1950b. Juvenile pattern in a mature *Coluber c. flaviventris*. Herpetologica, 6:124.

Neill, W. T.
1948. Hibernation of amphibians and reptiles in Richmond County, Georgia. Herpetologica, 4:107-114.

Odum, E. P. and Kuenzler, E. J.
1955. Measurement of territory and home range size in birds. Auk, 72:128-137.

Ortenburger, A. I.
1928. The whip snakes and racers, genera Masticophis and Coluber. Mem. Univ. Michigan Mus., vol. 1, pp. xviii + 247.

Owens, V.
1949. An overwintering colony of Coluber c. constrictor (Say) and Elaphe o. obsoleta (Say). Herpetologica, 5:90.

Parker, M. V.
1941. The trematode parasites from a collection of amphibians and reptiles. Jour. Tennessee Acad. Sci., 16(1):27-45.

Peters, J. A.
1942. Reptiles and amphibians of Cumberland County, Illinois. Copeia, 1942(3):182-183.

Pope, C. H.
1935. The reptiles of China. Amer. Mus. Nat. Hist., Nat. Hist. Cent. Asia, v. 10, lii + 604 pp.

1944. Amphibians and reptiles of the Chicago area. Chicago Nat. Hist. Mus. Press, 275 pp., 12 pls.

Pope, T. E. B. and Dickinson, W. E.
1928. The amphibians and reptiles of Wisconsin. Bull. Pub. Mus. City of Milwaukee, 8(1):1-138.

RICHMOND, N. D. and GOIN, C. J.
1938. Notes on a collection of amphibians and reptiles from New Kent County, Virginia. Ann. Carnegie Mus., 27:301-310.

ROSSMAN, D. A.
1960. Herpetological survey of the pine hills area of southern Illinois. Quart. Jour. Florida Acad. Sci. (1959), 22(4):207-225.

SCHMIDT, K. P. and NECKER, W. L.
1935. Amphibians and reptiles of the Chicago region. Bull. Chicago Acad. Sci., 5(4):57-77.

SCHRODER, R. C.
1950. Hibernation of blue racers and bull snakes in western Illinois. Nat. Hist. Misc., 75:1-2.

SHANNON, F. A.
1950. Coluber constrictor mormon—a state record for Arizona. Herpetologica, 6:59.

SMITH, H. M.
1956. Handbook of amphibians and reptiles of Kansas. Univ. Kansas Mus. Nat. Hist. Misc. Publ., 9:357 pp.

SMITH, P. W.
1947. The reptiles and amphibians of east central Illinois. Bull. Chicago Acad. Sci., 8(2):21-40.
1961. The amphibians and reptiles of Illinois. Bull. Illinois Nat. Hist. Surv., 28(1):1-298.

STAINS, H. J.
1956. The raccoon in Kansas. Univ. Kansas Mus. Nat. Hist. Misc. Publ., No. 10, pp. 1-76, pls. 1-4.

STEWART, P. L.
1959. Lung flukes of *Thamnophis* and *Coluber* in Kansas. Unpublished thesis University of Kansas Library, pp. 1-62.

STICKEL, W. H. and COPE, J. B.
1947. The home ranges and wandering of snakes. Copeia, 1947:127-136.

STORER, D. H.
1839. Reports on the ichthyology and herpetology of Massachusetts. Comm. Zool. and Bot. Surv. Mass., Boston, 201-258.

SURFACE, H. A.
1906. The serpents of Pennsylvania. Pennsylvania State Dept. Agr. Monthly Bull., Div. Zool., 4 (4 and 5):113-208.

TINKLE, D. W.
1959. Observations of reptiles and amphibians in a Louisiana swamp. Amer. Midl. Nat., 62(11):189-205.

TROWBRIDGE, A. H.
1937. Ecological observations on amphibians and reptiles collected in southeastern Oklahoma during the summer of 1934. Amer. Midl. Nat. 18(2):285-303.

UHLER, F. M., COTTAM, C. and CLARKE, T. E.
1939. Food of snakes of the George Washington National Forest, Virginia. Trans. 4th Amer. Wildlife Conf., Amer. Wildlife Inst., Washington, D. C., 1939:605-632.

VAN DENBURGH, J.
1923. The reptiles of western North America. Occas. Papers California Acad. Sci., 10:1-1028.

VAN DE VELDE, R. L., MARTAN, J. and RISLEY, P. L.
1962. Eggs and hatchlings of the snake *Coluber constrictor mormon* from Oregon. Copeia (1):212-213.

VERRILL, A. E.
1869. The biter bitten. Amer. Nat., 3:158-159.

Welter, W. A. and Carr, K.
1939. Amphibians and reptiles of northeastern Kentucky. Copeia (3): 128-130.

Werler, J. E. and McCallion, J.
1951. Notes on a collection of reptiles and amphibians from Princess Anne County, Virginia. Amer. Midl. Nat., 45(1):245-252.

Woodbury, A. M.
1931. A descriptive catalog of the reptiles of Utah. Bull. Univ. Utah, 21 (no. 5): x + 129 pp.

Woods, G. T.
1944. Black snake attacks a boy. Copeia, 1944(4):257.

Wright, A. H. and Bishop, S. C.
1915. A biological reconnaissance of the Okefinokee Swamp in Georgia. II. Snakes. Proc. Acad. Nat. Sci. Philadelphia, 67:139-192.

Wright, A. H. and Wright, A. A.
1957. Handbook of snakes of the United States and Canada. Comstock Publ. Associates, Cornell Univ. Press, vol. I, xviii + 564 pp.

Transmitted June 3, 1963.

29-4227

(Continued from inside of front cover)

18. Conspecificity of two pocket mice, Perognathus goldmani and P. artus. By E. Raymond Hall and Marilyn Bailey Ogilvie. Pp. 513-518, 1 map. January 14, 1960.
19. Records of harvest mice, Reithrodontomys, from Central America, with description of a new subspecies from Nicaragua. By Sydney Anderson and J. Knox Jones, Jr. Pp. 519-529. January 14, 1960.
20. Small carnivores from San Josecito Cave (Pleistocene), Nuevo León, México. By E. Raymond Hall. Pp. 531-538, 1 figure in text. January 14, 1960.
21. Pleistocene pocket gophers from San Josecito Cave, Nuevo León, México. By Robert J. Russell. Pp. 539-548, 1 figure in text. January 14, 1960.
22. Review of the insectivores of Korea. By J. Knox Jones, Jr., and David H. Johnson. Pp. 549-578. February 23, 1960.
23. Speciation and evolution of the pygmy mice, genus Baiomys. By Robert L. Packard. Pp. 579-670, 4 plates, 12 figures in text. June 16, 1960.

Index. Pp. 671-690

Vol. 10. 1. Studies of birds killed in nocturnal migration. By Harrison B. Tordoff and Robert M. Mengel. Pp. 1-44, 6 figures in text, 2 tables. September 12, 1956.
2. Comparative breeding behavior of Ammospiza caudacuta and A. maritima. By Glen E. Woolfenden. Pp. 45-75, 6 plates, 1 figure. December 20, 1956.
3. The forest habitat of the University of Kansas Natural History Reservation. By Henry S. Fitch and Ronald R. McGregor. Pp. 77-127, 2 plates, 7 figures in text, 4 tables. December 31, 1956.
4. Aspects of reproduction and development in the prairie vole (Microtus ochrogaster). By Henry S. Fitch. Pp. 129-161, 8 figures in text, 4 tables. December 19, 1957.
5. Birds found on the Arctic slope of northern Alaska. By James W. Bee. Pp. 163-211, plates 9-10, 1 figure in text. March 12, 1958.
*6. The wood rats of Colorado: distribution and ecology. By Robert B. Finley, Jr. Pp. 213-552, 34 plates, 8 figures in text, 35 tables. November 7, 1958.
7. Home ranges and movements of the eastern cottontail in Kansas. By Donald W. Janes. Pp. 553-572, 4 plates, 3 figures in text. May 4, 1959.
8. Natural history of the salamander, Aneides hardyi. By Richard F. Johnston and Gerhard A. Schad. Pp. 573-585. October 8, 1959.
9. A new subspecies of lizard, Cnemidophorus sacki, from Michoacán, México. By William E. Duellman. Pp. 587-598, 2 figures in text. May 2, 1960.
10. A taxonomic study of the middle American snake, Pituophis deppei. By William E. Duellman. Pp. 599-610, 1 plate, 1 figure in text. May 2, 1960.

Index. Pp. 611-626.

Vol. 11. Nos. 1-10 and index. Pp. 1-703, 1958-1960.

Vol. 12. 1. Functional morphology of three bats: Sumops, Myotis, Macrotus. By Terry A. Vaughan. Pp. 1-153, 4 plates, 24 figures in text. July 8, 1959.
*2. The ancestry of modern Amphibia: a review of the evidence. By Theodore H. Eaton, Jr. Pp. 155-180, 10 figures in text. July 10, 1959.
3. The baculum in microtine rodents. By Sydney Anderson. Pp. 181-216, 49 figures in text. February 19, 1960.
*4. A new order of fishlike Amphibia from the Pennsylvanian of Kansas. By Theodore H. Eaton, Jr., and Peggy Lou Stewart. Pp. 217-240, 12 figures in text. May 2, 1960.
5. Natural history of the bell vireo. By Jon C. Barlow. Pp. 241-296, 6 figures in text. March 7, 1962.
6. Two new pelycosaurs from the lower Permian of Oklahoma. By Richard C. Fox. Pp. 297-307, 6 figures in text. May 21, 1962.
7. Vertebrates from the barrier island of Tamaulipas, México. By Robert K. Selander, Richard F. Johnston, B. J. Wilks, and Gerald G. Raun. Pp. 309-345, pls. 5-8. June 18, 1962.
8. Teeth of Edestid sharks. By Theodore H. Eaton, Jr. Pp. 347-362, 10 figures in text. October 1, 1962.
9. Variation in the muscles and nerves of the leg in two genera of grouse (Tympanuchus and Pedioecetes). By E. Bruce Holmes. Pp. 363-474, 20 figs. October 25, 1963.
10. A new genus of Pennsylvanian Fish (Crossopterygii, Coelacanthiformes) from Kansas. By Joan Echols. Pp. 475-501, 7 figures. October 25, 1963.
11. Observations on the Mississippi Kite in southwestern Kansas. By Henry S. Fitch. Pp. 503-519. October 25, 1963.
12. Jaw musculature of the Mourning and White-winged doves. By Robert L. Merz. Pp. 521-551, 22 figures. October 25, 1963.

More numbers will appear in volume 12.

Vol. 13. 1. Five natural hybrid combinations in minnows (Cyprinidae). By Frank B. Cross and W. L. Minckley. Pp. 1-18. June 1, 1960.
2. A distributional study of the amphibians of the Isthmus of Tehuantepec, México. By William E. Duellman. Pp. 19-72, pls. 1-8, 3 figures in text. August 16, 1960.
3. A new subspecies of the slider turtle (Pseudemys scripta) from Coahulia, México. By John M. Legler. Pp. 73-84, pls. 9-12, 3 figures in text. August 16, 1960.
4. Autecology of the copperhead. By Henry S. Fitch. Pp. 85-288, pls. 13-20, 26 figures in text. November 30, 1960.
5. Occurrence of the garter snake, Thamnophis sirtalis, in the Great Plains and Rocky Mountains. By Henry S. Fitch and T. Paul Maslin. Pp. 289-308, 4 figures in text. February 10, 1961.

(Continued on outside of back cover)

(Continued from inside of back cover)

6. Fishes of the Wakarusa river in Kansas. By James E. Deacon and Artie L. Metcalf. Pp. 309-322, 1 figure in text. February 10, 1961.
7. Geographic variation in the North American cyprinid fish, Hybopsis gracilis. By Leonard J. Olund and Frank B. Cross. Pp. 323-348, pls. 21-24, 2 figures in text. February 10, 1961.
8. Decriptions of two species of frogs, genus Ptychohyla; studies of American hylid frogs, V. By William E. Duellman. Pp. 349-357, pl. 25, 2 figures in text. April 27, 1961.
9. Fish populations, following a drought, in the Neosho and Marais des Cygnes rivers of Kansas. By James Everett Deacon. Pp. 359-427, pls. 26-30, 3 figs. August 11, 1961.
10. Recent soft-shelled turtles of North America (family Trionychidae). By Robert G. Webb. Pp. 429-611, pls. 31-54, 24 figures in text. February 16, 1962.

Index. Pp. 613-624.

Vol. 14. 1. Neotropical bats from western México. By Sydney Anderson. Pp. 1-8. October 24, 1960.
2. Geographic variation in the harvest mouse. Reithrodontomys megalotis, on the central Great Plains and in adjacent regions. By J. Knox Jones, Jr., and B. Mursaloglu. Pp. 9-27, 1 figure in text. July 24, 1961.
3. Mammals of Mesa Verde National Park, Colorado. By Sydney Anderson. Pp. 29-67, pls. 1 and 2, 3 figures in text. July 24, 1961.
4. A new subspecies of the black myotis (bat) from eastern Mexico. By E. Raymond Hall anad Ticul Alvarez. Pp. 69-72, 1 figure in text. December 29, 1961.
5. North American yellow bats, "Dasypterus," and a list of the named kinds of the genus Lasiurus Gray. By E. Raymond Hall and J. Knox Jones, Jr. Pp. 73-98, 4 figures in text. December 29, 1961.
6. Natural history of the brush mouse (Peromyscus boylii) in Kansas with description of a new subspecies. By Charles A. Long. Pp. 99-111, 1 figure in text. December 29, 1961.
7. Taxonomic status of some mice of the Peromyscus boylii group in eastern Mexico, with description of a new subspecies. By Ticul Alvarez. Pp. 113-120, 1 figure in text. December 29, 1961.
8. A new subspecies of ground squirrel (Spermophilus spilosoma) from Tamaulipas, Mexico. By Ticul Alvarez. Pp. 121-124. March 7, 1962.
9. Taxonomic status of the free-tailed bat, Tadarida yucatanica Miller. By J. Knox Jones, Jr., and Ticul Alvarez. Pp. 125-133, 1 figure in text. March 7, 1962.
10. A new doglike carnivore, genus Cynaretus, from the Clarendonian Pliocene, of Texas. By E. Raymond Hall and Walter W. Dalquest. Pp. 135-138, 2 figures in text. April 30, 1962.
11. A new subspecies of wood rat (Neotoma) from northeastern Mexico. By Ticul Alvarez. Pp. 139-143. April 30, 1962.
12. Noteworthy mammals from Sinaloa, Mexico. By J. Knox Jones, Jr., Ticul Alvarez, and M. Raymond Lee. Pp. 145-159, 1 figure in text. May 18, 1962.
13. A new bat (Myotis) from Mexico. By E. Raymond Hall. Pp. 161-164, 1 figure in text. May 21, 1962.
14. The mammals of Veracruz. By E. Raymond Hall anad Walter W. Dalquest. Pp. 165-362, 2 figures. May 20, 1963.
15. The recent mammals of Tamaulipas, México. By Ticul Alvarez. Pp. 363-473, 5 figures in text. May 20, 1963.

More numbers will appear in volume 14.

Vol. 15. 1. The amphibians and reptiles of Michoacán, México. By William E. Duellman. Pp. 1-148, pls. 1-6, 11 figures in text. December 20, 1961.
2. Some reptiles and amphibians from Korea. By Robert G. Webb, J. Knox Jones, Jr., and George W. Byers. Pp. 149-173. January 31, 1962.
3. A new species of frog (Genus Tomodactylus) from western México. By Robert G. Webb. Pp. 175-181, 1 figure in text. March 7, 1962.
4. Type specimens of amphibians and reptiles in the Museum of Natural History, the University of Kansas. By William E. Duellman and Barbara Berg. Pp. 183-204. October 26, 1962.
5. Amphibians and Reptiles of the Rainforests of Southern El Petén, Guatemala. By William E. Duellman. Pp. 205-249, pls. 7-10, 6 figures in text. October 4, 1963.
6. A revision of snakes of the genus Conophis (Family Colubridae, from Middle America). By John Wellman. Pp. 251-295, 9 figures in text. October 4, 1963.
7. A review of the Middle American tree frogs of the genus Ptychohyla. By William E. Duellman. Pp. 297-349, pls. 11-18, 7 figures in text. October 18, 1963.
8. Natural history of the racer, Coluber constrictor. By Henry S. Fitch. Pp. 351-468, pls. 19-22, 20 figures. December 30, 1963.

More numbers will appear in volume 15.

LIBRARY
JUL 21 1964
HARVARD
UNIVERSITY

University of Kansas Publications
Museum of Natural History

Volume 15, No. 9, pp. 469-491, 4 figs.
March 2, 1964

A Review of the Frogs Of the Hyla bistincta Group

BY

WILLIAM E. DUELLMAN

University of Kansas
Lawrence
1964

University of Kansas Publications, Museum of Natural History
Editors: E. Raymond Hall, Chairman, Henry S. Fitch,
Theodore H. Eaton, Jr.

Volume 15, No. 9, 469-491, 4 figs.
Published March 2, 1964

University of Kansas
Lawrence, Kansas

PRINTED BY THE STATE PRINTER
TOPEKA, KANSAS
1964
29-8590

MUS. COMP. ZOOL
LIBRARY
JUL 21 1964
HARVARD
UNIVERSITY

A Review of the Frogs Of the Hyla bistincta Group

BY

WILLIAM E. DUELLMAN

CONTENTS

PAGE

INTRODUCTION 471
Acknowledgments 471
THE HYLA BISTINCTA GROUP 472
Analysis of Characters 473
Key to the Species of the Hyla Bistincta Group 474
ACCOUNTS OF THE SPECIES 475
Hyla bistincta Cope 475
Hyla charadricola new species 478
Hyla robertsorum Taylor 481
Hyla pachyderma Taylor 485
Hyla crassa (Brocchi) 486
RELATIONSHIPS 489
LITERATURE CITED 491

INTRODUCTION

In the mountainous regions of Middle America there are several groups of hylid frogs that inhabit mountain streams. Some of these groups, such as *Plectrohyla* and *Ptychohyla,* have been elevated to generic rank, whereas others are retained in the large and complex genus *Hyla.* In the mountains of México five species of hylids that seem to compose a phyletic unit are herein referred to as the *Hyla bistincta* group. Since 1955 I have been accumulating specimens of, and data on, this group with the result that all specimens known to me, including the types of all named taxa, have been studied. Detailed observations have been made on the ecology and life histories of three of the species; the other two species are known to me only from preserved specimens.

Acknowledgments

For permission to examine specimens in their care I am indebted to Charles M. Bogert, American Museum of Natural History (AMNH); Doris M. Cochran, United States National Museum (USNM); Jean Guibé, Museum National d'Histoire Naturelle, Paris (MNHN); Robert F. Inger, Chicago Natural History Museum (CNHM); Hobart M. Smith, University of Illinois Museum of Natural History (UIMNH); Charles F. Walker, University of Michigan Museum of Zoology (UMMZ). (Abbreviations of institutions given above in parentheses are used throughout; the Museum of Natural History, University of Kansas is abbreviated KU.)

For their willing assistance in the field I am grateful to Ann S. Duellman, Dale L. Hoyt, and John Wellman. Permits for collecting in México were generously issued by the late Ing. Luis Macías Arellano, Departamento de la Fauna Silvestre, Dirección General de Caza. The drawings in figures 1 and 3 were executed by Gail Selfridge. This research has been supported by the National Science Foundation (NSF G-9827).

THE HYLA BISTINCTA GROUP

The five species comprising the *Hyla bistincta* group are moderate-sized hylids having rather blunt heads and robust bodies. The fingers are long and have little webbing (Fig. 1). The skin of the dorsum is thick and glandular, but not tuberculate. An anal sheath is present. The skull is rather broad, flat, and solidly roofed. The ethmoid is broad, curved downward laterally, and solidly sutured to the frontoparietal. The nasals are broad, sutured for their entire width with the ethmoid, and broadly in contact medially. The premaxillaries are in contact medially; each has a long, flat nasal process. The quadratojugal is absent, and the maxillary tapers to a point posteriorly. There is no squamosal-maxillary connection. The maxillary and premaxillary teeth are rather long, bifid, and moderately spatulate. Some teeth on the premaxillary and anterior part of the maxillary are hooked. The vomerine teeth are spatulate and bifid. A broad, flat, ossified prepollex is present but does not project as a spine. The known tadpoles have ventral mouths, 2/3 tooth-rows, two or more rows of labial papillae, and long tails with low fins.

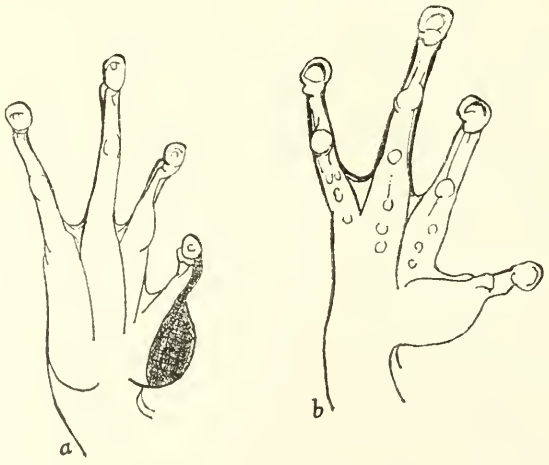


FIG. 1. Palmar view of right hand of: *a.—Hyla robertsorum* (KU 57661), *b.—Hyla charadricola* (KU 58414). × 3.

As thus defined the *Hyla bistincta* group can be distinguished from all other groups of Middle American frogs by the combination of absence of the quadratojugal, non-projecting prepollex, long fingers with little webbing, and stream-inhabiting tadpoles having 2/3 tooth rows and two or more rows of labial papillae.

Possibly *Hyla arborescandens* and *Hyla hazelae* belong in this group. Because these species are somewhat different from the included species and because their tadpoles are as yet unknown, I have refrained from including these two species in the *Hyla bistincta* group. Taylor (1948:261) assigned *Hyla proboscidea* (= *H. dalquesti*) and (1949:272) *Hyla cyclomaculata* to this group, but because these two species have a quadratojugal and notably different tadpoles, they are excluded from the group.

Frogs of the genus *Plectrohyla* closely resemble species in the *Hyla bistincta* group but differ principally in having a projecting prepollex. In the highlands of Costa Rica a group of species, of which *Hyla moesta* is best known, resembles species in the *Hyla bistincta* group. At present insufficient information is available on the Costa Rican species to determine their affinities.

Analysis of Characters

The characters used in the systematic study of the frogs in this group are those usually employed in anuran systematics. Of the various measurements and proportions, the snout-vent length and the relative size of the tympanum to the eye apparently are of more taxonomic importance than the others (Table 1). In all of the species the tympanum is at least partially covered by a heavy, dermal supratympanic fold, and in some specimens of *H. pachyderma* the tympanum is completely obscured. In two species (*H. bistincta* and *H. charadricola*) the snout is square, whereas in the other species it is round.

The fingers are long and slender in *H. crassa, pachyderma,* and *robertsorum* and somewhat shorter with more webbing in *H. bistincta* and *charadricola.* Breeding males of *Hyla pachyderma* have moderately large nuptial spines; the other species have small spines, except *H. charadricola* in which spines apparently are absent. A well-defined thoracic fold is present in *H. pachyderma,* and a weak fold is present in *H. robertsorum;* the other species lack folds. In all species there is an anal sheath; this sheath is longest in *H. bistincta,* in which the anal opening is directed ventrally at the level of the lower edge of the thighs.

TABLE 1.—COMPARISON OF CERTAIN MEASUREMENTS AND PROPORTIONS IN THE SPECIES OF THE HYLA BISTINCTA GROUP. (DATA FROM ADULT MALES; MEANS ARE GIVEN IN PARENTHESES BELOW THE RANGES.)

SPECIES	N	Snout-vent length	Tibia length / Snout-vent length	Head width / Snout-vent length	Tympanum / Eye
H. bistincta	38	43.0–53.8 (46.3)	0.47–0.52 (0.49)	0.32–0.37 (0.34)	0.35–0.48 (0.42)
H. charadricola	10	35.3–44.4 (40.4)	0.50–0.54 (0.52)	0.31–0.33 (0.32)	0.30–0.37 (0.34)
H. robertsorum	26	39.9–47.9 (43.1)	0.48–0.51 (0.49)	0.30–0.36 (0.32)	0.36–0.47 (0.41)
H. pachyderma	1	39.9	0.53	0.32	...
H. crassa	1	53.7	0.50	0.33	0.28

Frogs in this group are rather drab in appearance. The dorsal color varies from dull green to various shades of brown. The most distinct aspect of the coloration is the different color patterns on the flanks and posterior surfaces of the thighs. The flanks in all species are marked with spots or reticulations.

Hyla bistincta differs from other members of the group in having vocal slits and a distensible vocal sac. Only this species has been reported to call (Shannon, 1951:473). Insofar as is known, the other species are mute. Examination of skeletal preparations of *H. bistincta, charadricola,* and *robertsorum* and X-rays of the other species shows no notable specific differences in the osteology. Since the tadpoles of only *H. bistincta* (Duellman, 1961:47) and *H. robertsorum* (Rabb and Mosimann, 1955) are known, larval characters are of limited use in intra-group systematics.

Key to the Species of the *Hyla bistincta* Group

1. Snout, in dorsal profile, short and bluntly rounded; canthus rounded, sometimes indistinct, vocal slits absent 2
   Snout, in dorsal profile, longer, squared; canthus distinct, vocal slits present or absent 4
2. Feet webbed to base of discs; dorsum dull olive green; flanks having cream-colored spots ..... *H. crassa,* p. 486
   Feet not webbed to base of discs; dorsum brown 3
3. Tarsal fold strong; thoracic fold heavy; webbing on feet extending to middle of penultimate phalanx of fourth toe; distinct white stripe above anus; cluster of large spines on thumb in breeding males, *H. pachyderma,* p. 485

Tarsal fold weak and short; thoracic fold absent or barely indicated; webbing of feet extending to base of penultimate phalanx of fourth toe; no distinct white stripe above anus; nuptial tuberosities in breeding males consisting of small spines ..... *H. robertsorum*, p. 481

4. Tarsal fold strong; anal flap elongate; anus opening at lower edge of femur; dorsum tan or brown; flanks mottled with cream and brown; venter immaculate creamy white; no anal stripe; vocal slits present, *H. bistincta*, p. 475

Tarsal fold faint and short; anal flap not elongate; anus opening at middle of femur; dorsum olive-green with black reticulations; flanks greenish gray with brown or black spots; a row of white flecks above and below anus, vocal slits absent ..... *H. charadricola*, p. 478

ACCOUNTS OF THE SPECIES

In the following accounts complete synonymies are given for each species. In each account one specimen is described in detail; after this description the variation is discussed. In the list of specimens examined, localities are arranged alphabetically within the states, which also are given in alphabetical order. Localities given in italics are not shown on the accompanying maps (Figs. 2 and 4) due to crowding of symbols.

Hyla bistincta Cope

Hyla bistincta Cope, Proc. Amer. Philos. Soc., 17:87, August, 1877 [Holotype.—USNM 32261 from "most probably Veracruz," México; Francis Sumichrast collector]. Brocchi, Étude des batraciens de l'Amérique Centrale, p. 43, 1881. Boulenger, Catalogue Batrachia Salientia, 2nd Ed., p. 401, February 1, 1882. Sumichrast, La Naturaleza, 6:81, 1882. Cope, Bull. U. S. Natl. Mus., 32:14, 1887; Bull. U. S. Natl. Mus., 34:351, 1889. Günther, Biologia Centrali-Americana, Reptilia and Batrachia, pp. 265-6, June, 1901. Díaz de León, Indice de los batracios que se encuentran en la República Mexicana, p. 17, June, 1904. Nieden, Das Tierreich, Amphibia, Anura I, p. 247, June, 1923. Kellogg, Bull. U. S. Natl. Mus., 160:163-164, March 31, 1932. Taylor, Proc. Biol. Soc. Washington, 50:50-53, April 21, 1937; Univ. Kansas Sci. Bull., 26:389, November 27, 1940. Taylor and Smith, Proc. U. S. Natl. Mus., 194:87, June 7, 1948. Taylor, Univ. Kansas Publ. Mus. Nat. Hist., 1:261, August 16, 1948; Copeia, no. 4:272-273, December 15, 1949. Smith and Taylor, Univ. Kansas Sci. Bull., 33:346, March 20, 1950 [Type locality restricted to Acultzingo, Veracruz, México]. Rabb and Mosimann, Occas. Papers Mus. Zool. Univ. Michigan, 563:6-9, March 29, 1955. Duellman, Univ. Kansas Publ. Mus. Nat. Hist., 15:47-49, December 20, 1961.

Hyla bistincta labeculata Shannon, Proc. U. S. Natl. Mus., 101:470-473, figs. 92a, 93d, May 17, 1951 [Holotype.—USNM 123689 from San Lucas Camotlán, Oaxaca, México; Walter S. Miller collector]. Smith and Williams, Herpetologica, 19:23, April 11, 1963.

Hyla bistincta bistincta, Shannon, Proc. U. S. Natl. Mus., 101:472, May 17, 1951. Shannon and Werler, Herpetologica, 11:85, July 15, 1955. Smith and Williams, Herpetologica, 19:23, April 11, 1963.

Diagnosis.—Maximum snout-vent length in males 54 mm.; snout in dorsal profile truncate; tarsal fold strong; inner metatarsal tubercle large, high, and elongate; outer metatarsal tubercle absent; webbing on foot extending to middle of antepenultimate phalanx of fourth toe; nuptial spines on thumb small; thoracic fold absent; anal opening at level of lower edge of femur; dorsum

brown or tan; belly cream-color; flanks creamy yellow with brown reticulations or spots; anal stripe absent; vocal slits present.

Description.—The following description is based on KU 68078 from Uruapan, Michoacán, México. Adult male having a snout-vent length of 43.2 mm.; tibia length, 22.1 mm., 51.1 per cent of snout-vent length; foot length (measured from proximal edge of inner metatarsal tubercle to tip of longest toe), 20.8 mm.; greatest width of head, 15.4 mm., 35.6 per cent of snout-vent length; head length, 13.9 mm., 32.1 per cent of snout-vent length; diameter of eye, 5.1 mm.; diameter of tympanum, 2.4 mm., 47.1 per cent of diameter of eye. Snout in lateral profile bluntly rounded, in dorsal profile truncate; canthus pronounced, rounded, not angular; loreal region slightly concave; lips thick, round, not flaring; nostrils slightly protuberant; internarial distance, 3.4 mm.; interorbital distance, 4.5 mm., somewhat broader than width of eyelid, 3.5 mm. A heavy dermal fold from posterior corner of eye above tympanum and curved downward to insertion of forearm; tympanum round, its diameter slightly more than its distance from eye. Forearm not robust; row of small pustules on ventral surface of forearm; fold on wrist; prepollex moderately enlarged, covered with small, horny, nuptial spines continuous on edge of digit; row of spines on inner surface of second finger; subarticular tubercles large, round, none bifid; supernumerary tubercles rather large, round; palmar tubercles rather small, flat, elliptical; fingers long, moderately slender; length of fingers from shortest to longest, 1-2-4-3; discs moderately large, that on third finger slightly larger than tympanum; rudimentary web between first and second and between second and third fingers; web between third and fourth fingers extending about one-fourth length of fourth finger. Heels overlap by about one-third length of shank when hind limbs adpressed; tibiotarsal articulation extends to anterior edge of eye; tarsal fold strong, extending to heel; inner metatarsal tubercle large, high, and elongate; outer metatarsal tubercle absent; subarticular tubercles moderately large, round; supernumerary tubercles small, in single rows on proximal segments of digits; toes moderately short; length of toes from shortest to longest, 1-2-3-5-4, third and fifth toes about equal in length; toes about two-thirds webbed; web extending to middle of antepenultimate phalanx of fourth toe, to discs of first, second, and fifth toes, and to base of penultimate phalanx of third toe; discs rather small, about two-thirds size of those on fingers. Anal opening at level of lower edge of thighs; anal sheath elongate, deeply creased medially; transverse dermal fold above anus. Skin of dorsal surfaces of head, body, and limbs faintly areolate; skin of chin, belly, and ventral surfaces of thighs granular, that of ventral surfaces of limbs, except thighs, areolate; thoracic fold absent. Tongue nearly round, slightly longer than wide, shallowly notched behind and barely free posteriorly. Vomerine teeth 4-4, situated on rounded vomerine ridges between rather small ovoid inner nares; vocal slits present, situated along posterior edge of each ramus.

Color (in alcohol) pale brown on dorsal surfaces of head, body, and limbs; flanks and anterior surfaces of thighs creamy white with dark brown reticulations; posterior surfaces of thighs tan with creamy white spots; belly cream-color; anal stripe absent.

Color (in life) pale tan on dorsal surfaces; flanks and anterior surfaces of thighs pale creamy yellow with purplish brown reticulations; posterior surfaces of thighs tan with yellow spots; ventral surfaces yellow; iris pale copper-color.

Variation.—There is little variation in structure. The total number of vomerine teeth varies from 6 to 14. In some individuals the supratympanic fold covers the upper part of the tympanum, but at least the lower part of the tympanum is always visible. The extent of the webbing between the toes varies from three-fourths to two-thirds complete. Usually the web extends to some point on the antepenultimate phalanx of the fourth toe, but in some specimens the web extends to the base of the penultimate phalanx.

In the large series of specimens from Uruapan, Michoacán, the coloration of the flanks and anterior surfaces of the thighs varies from nearly uniform creamy yellow with only fine dark reticulations to bold reticulations enclosing yellow spots. Some specimens from Oaxaca and Veracruz have slightly different markings on the flanks; in these the dark pigment is in the form of irregular spots or dashes, instead of reticulations.

There is considerable variation in color in the living frogs. The dorsum varies from greenish tan and pale yellowish tan to reddish brown, and some individuals are dark chocolate brown.

Remarks.—Shannon (1951:470) named *Hyla bistincta labeculata* on the basis of a single male from San Lucas Camotlán, Oaxaca; he diagnosed the subspecies as differing from *Hyla bistincta bistincta* by having "the gray reticulation of the sides entirely broken up into elongate black blotches; tarsal fold moderately elevated." The condition of the tarsal fold is characteristic of the species. The dispersion of dark pigment on the flanks is variable. The type of *Hyla bistincta labeculata* (USNM 123689) is extreme in the development of dark dashes on the flanks, but this condition is approached in several specimes from Oaxaca and Veracruz. For example, in some specimens from Cumbres de Acultzingo, Veracruz, the mottling on the flanks is bold; in others the flanks are reticulated. The specimen from San Vicente, Oaxaca, has black dashes on the flanks (Smith and Williams, 1963:23), whereas a specimen from Cerro San Felipe, Oaxaca, has no pattern on the flanks. In general, specimens from western México have reticulate mottling on the flanks as compared with the marbling on the flanks in specimens from eastern México. On the basis of available data, the recognition of subspecies in *Hyla bistincta* is unwarranted.

The tadpoles of this species described by Duellman (1961:47) are like those of *Hyla robertsorum* in having 2/3 tooth-rows, peglike serrations on the beaks, and long, rounded tails. At Uruapan tadpoles were found in a rocky stream on April 24, 1956, and metamorphosing young were found there on August 2, 1956. A completely metamorphosed juvenile has a snout-vent length of 24.8 mm.

Hyla bistincta is found only along streams, where individuals can be seen clinging to vines and other vegetation closely over-hanging fast-moving parts of the stream.

Distribution.—*Hyla bistincta* occurs at elevations from 1400 to 2600 meters in the mountains of the Sierra Madre Occidental in western Jalisco southward through the Cordillera Volcánica in Michoacán, México, and Morelos, the Sierra de Coalcomán in Michoacán, and the Sierra Madre del Sur in Guerrero and Oaxaca, and thence northward in the Sierra Madre Oriental to central Veracruz (Fig. 2).

Specimens examined.—GUERRERO: Omiltemi, UIMNH 38023-5. JALISCO: 25 km. SE Autlán, UMMZ 102076. MEXICO: 19 km. W Villa Victoria, UIMNH 28162, USNM 114513. MORELOS: Cuernavaca, USNM 121523; *3 km. N Cuernavaca,* UIMNH 28168-70. MICHOACAN: Cerro San Andrés, UMMZ 102075; Dos Aguas, UMMZ 119193; *12.5 km. ENE Dos Aguas,* UMMZ 119194; *Los Conejos,* UMMZ 94238-40; Uruapan, KU 68077-8, 69093 (skeleton), UIMNH 20457, 28167, UMMZ 85452-3, 112838, 112839 (16), 115231 (tadpoles), 115232, 115233 (12), 121515, S-1699 (skeleton), S-1826 (skeleton), USNM 114514-5, 114517-24. OAXACA: Cerro San Felipe, UIMNH 28163; Pluma Hidalgo, AMNH 13447; San Lucas Camotlán, USNM 123689; San Vincente, UIMNH 51346 (Smith and Williams, 1963:23). VERACRUZ: no specific locality, USNM 32261; Cumbres de Acultzingo, CNHM 105482-3, UIMNH 28164-6, 49133-4, USNM 114525.

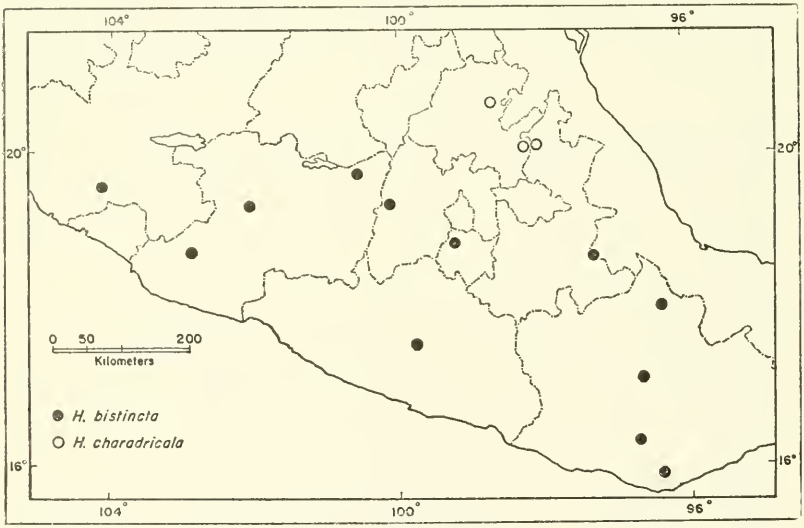


FIG. 2. Map showing locality records for *Hyla bistincta* and *Hyla charadricola.*

Hyla charadricola new species

Holotype.—University of Kansas Museum of Natural History No. 58414 from the Río Totolapa, 14.4 kilometers by road west of Huachinango, Puebla, México, 2280 meters; obtained by John Wellman on June 8, 1960.

Paratypes.—KU 58415-58423, same data as holotype, and UIMNH 50966, obtained at the type locality by William E. Duellman on February 11, 1961.

Diagnosis.—Maximum snout-vent length in males, 45 mm.; snout in dorsal profile truncate; tarsal fold short and weak; inner metatarsal tubercle moderately large, elliptical, and flat; outer metatarsal tubercle minute, round, and indistinct; webbing extending to base of terminal phalanx of fourth toe; nuptial

spines on thumb absent; thoracic fold absent; anal opening at level of middle of thigh; dorsum olive-green with black reticulations; venter cream color with brown flecks on chin; flanks pale grayish green with brown spots; anal stripe absent; row of white flecks above and a row below anus; vocal slits absent.

Description of Holotype.—Adult male having a snout-vent lenth of 44.4 mm.; tibia length, 22.2 mm., 50 per cent of snout-vent length; foot length (measured from proximal edge of inner metatarsal tubercle to tip of longest toe), 20.4 mm.; greatest width of head, 14.0 mm., 31.5 per cent of snout-vent length; head length, 13.6 mm., 30.6 per cent of snout-vent length; diameter of eye, 5.0 mm.; diameter of tympanum, 1.6 mm., 32.0 per cent of diameter of eye. Snout in lateral profile bluntly rounded, in dorsal profile truncate (Fig. 3); canthus pronounced, rounded, not angular; loreal region slightly concave; lips thick, rounded, not flaring; nostrils slightly protuberant; internarial distance, 3.7 mm.; interorbital distance, 4.1 mm., somewhat broader than width of eyelid, 3.3 mm. A heavy dermal fold from posterior corner of eye above tympanum and then to insertion of forearm; tympanum round, its diameter three-fourths its distance from eye. Forearm rather slender; a short axillary membrane; no fold on wrist; no nuptial excrescence or spines on enlarged prepollex; subarticular tubercles moderately small, round; none bifid; few supernumerary tubercles on proximal segments of digits; large, flat palmar tubercle present; fingers long and slender; length of fingers from shortest to longest, 1-2-4-3; discs moderately large, that on third finger about equal to diameter of tympanum; rudimentary web between first and second fingers; web between third and fourth fingers extending to about one-fifth length of fourth finger (Fig. 1). Heels overlap by about one-third length of tibia when hind limbs adpressed; tibiotarsal articulation extends to middle of eye; tarsal fold weak, extending from moderately large, flat, elliptical inner metatarsal tubercle to middle of tarsus; outer metatarsal tubercle minute, round, indistinct; subarticular tubercles round; single row of small, round supernumerary tubercles on proximal segments of each digit; toes moderately short and slender; length of toes from shortest to longest, 1-2-3-5-4, third and fifth about equal in length; toes about three-fourths webbed; web extending to base of terminal phalanx of fourth toe; discs small, about two-thirds size of those on fingers. Anal opening directed posteroventrally at middle of thighs; two transverse dermal folds above anus; short, thin anal sheath present; many small tubercles lateral and ventral to anal opening. Skin of dorsum, chin, and ventral surfaces of limbs smooth; belly moderately granular; posterior surfaces of thighs heavily granular; no thoracic fold. Tongue nearly round, shallowly notched behind, free posteriorly for about one-fourth its length; vomerine teeth, 3-4, long, situated on posteroventral edges of narrow transverse vomerine ridges between moderately large, round inner nares; no vocal slits.

Color (in alcohol) purplish brown on dorsal surfaces of head, body, and limbs; fine darker reticulations on dorsum; flanks pale tan with dark brown spots; posterior surfaces of thighs tan; chin creamy white with brown spots; belly dusty white; undersides of thighs and shanks yellow; webbing grayish brown; undersides of first two fingers dusty white, of third and fourth fingers and of feet brown; anal stripe absent; small white flecks above and below anal opening.

Color (in life) dark green on dorsal surfaces of head, body, and limbs; darker green reticulations on back; flanks dusty white with dark olive-gray

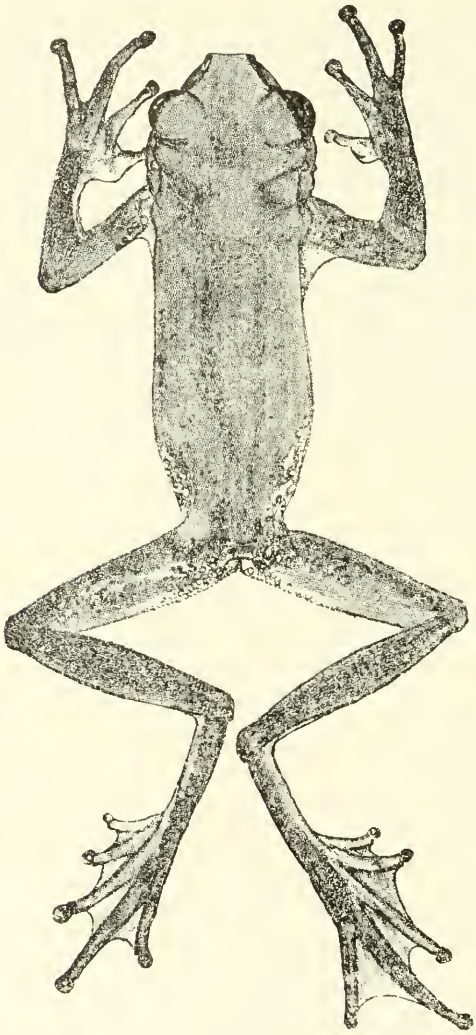


FIG. 3. Holotype of *Hyla charadricola* (KU 58414). × 1.5.

mottling; dark olive-gray stripe from nostril through eye and then to insertion of forelimb; upper lips pale green; inguinal region, anterior and posterior surfaces of thighs dark yellowish orange; ventral surfaces of tarsi and shanks, and webbing of feet dusty yellow; belly white; iris silvery gold.

Variation.—Adult males have snout-vent lengths from 35.3 to 44.4 mm., and adult females from 43.4 to 50.9 mm. No notable variation in structure is displayed in the type series. In some individuals the dark reticulation on the dorsum is faint. Juveniles in life had dorsal colorations varying from rich brown with darker reticulations to pale green or gray with dark green reticula-

tions. Some adults when collected were pale green with faint or no dorsal reticulations; later these individuals darkened. In all specimens the anal stripe is absent, and the flanks are heavily spotted.

Comparisons.—Hyla charadricola differs from all other members of the *Hyla bistincta* group in the following combination of characters: truncate snout, green dorsum, and absence of a thoracic fold. From other hylids that occur in the same area, *Hyla charadricola* differs from *Hyla miotympanum* and *H. arborescandens,* both of which are green dorsally, by having a truncate snout and longer fingers with less webbing. *Hyla eximia,* though green, has brown dorsal spots, shorter fingers, and a round snout. *Hyla robertsorum* differs in having a round snout and brown dorsum, and *Hyla taeniopus* is much larger, has transverse bands on the limbs, and has extensive webbing between fingers.

Remarks.—At the type locality, a shallow rocky stream in pine forest, *Hyla charadricola* was found beneath rocks at the edge of fast moving sections of the stream and beneath rocks in shallow riffles in the stream. Most of the frogs were in water. At night they were found sitting on rocks in the stream. *Hyla miotympanum,* which is abundant at the type locality, lives in bushes and beneath rocks along the stream but usually is not found in the riffles inhabited by *Hyla charadricola.* At Lago de Tejocotal *Hyla charadricola* was found beneath rocks near the shore of the lake and by a stream in the pine forest. Individuals were found on low vegetation over-hanging a small stream in pine-oak forest four kilometers southwest of Tianguistengo.

Five recently metamorphosed young (KU 58424-9) found at the type locality on June 8, 1960, have snout-vent lengths of 22.4 to 24.0 (average 23.2) mm. The young are colored like the adults, except that in life the dorsum is a brighter green and the flanks are more yellow than tan and have less dark spotting than in adults.

Distribution.—Hyla charadricola inhabits streams in pine and pine-oak forests at elevations of 2000 to 2300 meters in northern Puebla and eastern Hidalgo (Fig. 2).

Specimens examined.—HIDALGO: Lago de Tejocotal, 11 km. E Acaxochitlán, KU 58438, UMMZ 104032, 118165; 4 km. SW Tianguistengo, KU 53811-2. PUEBLA: *11.7 km. W Huachinango,* UMMZ 121567 (5); Río Totolapa, 14.4 km. W Huachinango, KU 53813-5, 55624, 58414-37, 59813 (skeleton), 59886 (skeleton), MCZ 34964-5, UIMNH 50966, UMMZ 118166 (5), S-2242 (skeleton).

Hyla robertsorum Taylor

Hyla robertsorum Taylor, Univ. Kansas Sci. Bull., 26:393-396, figs. 5-6, November 27, 1940 [Holotype.—CNHM 100124 (formerly EHT-HMS 16264) from El Chico Parque Nacional, Hidalgo, México; Mr. and Mrs. Radclyffe Roberts and Edward H. Taylor collectors]; Univ. Kansas Sci. Bull., 28:310, November 15, 1942. Taylor and Smith, Proc. U. S. Natl. Mus., 95:589, June 30, 1945. Smith and Taylor, Bull. U. S. Natl. Mus., 194:87, June 17, 1948; Univ. Kansas Sci. Bull., 33:333, March 20, 1950. Rabb and Mosimann, Occas. Papers Mus. Zool. Univ. Michigan, 563:1-9, March 29, 1955. Duellman, Univ. Kansas Publ. Mus. Nat. Hist., 15:48, December 20, 1961.

Diagnosis.—Maximum snout-vent length in males, 48 mm.; snout in dorsal profile rounded; tarsal fold short and weak; inner metatarsal tubercle moderate in size and elliptical; outer metatarsal tubercle small, round, and indistinct; webbing extending to base of penultimate phalanx of fourth toe; nuptial spines on thumb small; weak thoracic fold present; anal opening above level of middle of thighs; dorsum dark brown with dark reticulations; venter brown with cream-colored flecks; flanks brown with creamy white spots; anal stripe absent; small white spots in anal region; vocal slits absent.

Description.—The following description is based on KU 57651 from El Chico Parque Nacional, Hidalgo. Adult male having a snout-vent length of 45.1 mm.; tibia length, 22.1 mm., 49.0 per cent of snout-vent length; foot length (measured from proximal edge of inner metatarsal tubercle to tip of longest toe), 21.5 mm.; greatest width of head, 13.7 mm., 30.4 per cent of snout-vent length; head length, 12.6 mm., 27.9 per cent of snout-vent length; diameter of eye, 4.0 mm.; diameter of tympanum, 1.8 mm., 45 per cent of diameter of eye. Snout short, in lateral profile blunt, in dorsal profile round; canthus rounded; loreal region slightly concave; lips thick, round, and not flaring; nostrils slightly protuberant; internarial distance, 3.6 mm.; interorbital distance, 4.0 mm., slightly broader than width of eyelid, 3.5 mm. A moderately heavy dermal fold from posterior corner of eye above tympanum and curving downward towards insertion of forearm; tympanum nearly round, covered by dermal fold above, its diameter slightly less than its distance from eye. Forearm moderately robust; distinct fold on wrist; prepollex much enlarged with patch of small nuptial spines continuous on side of digit; similar line of nuptial spines on inner edge of second finger; subarticular tubercles round, moderate in size, none bifid; supernumerary tubercles small and present only proximally; fingers long and slender; length of fingers from shortest to longest, 1-2-4-3; discs moderately large, that on third finger about size of tympanum; no web between first and second fingers; rudimentary web between other fingers. Legs robust; heels over-lap by about one-fourth length of shank when hind limbs adpressed; tibiotarsal articulation extending to posterior corner of eye; tarsal fold weak, extending to about middle of tarsus; inner metatarsal tubercle moderately large, flat, and elliptical; outer metatarsal tubercle small, round, and indistinct; subarticular tubercles round; supernumerary tubercles small, in single row on proximal segments of each digit; toes moderately long and slender; length of toes from shortest to longest, 1-2-5-3-4, the fifth nearly as long as third; toes nearly fully webbed; web extending to base of penultimate phalanx of fourth toe and to discs on other toes; discs small, about two-thirds size of those on fingers. Anal opening above middle of thighs; anal sheath short, deeply creased medially; heavy transverse dermal fold above anus; no large anal tubercles. Skin of all dorsal surfaces, chin, and ventral surfaces of limbs, except proximal parts of thighs, smooth; belly and proximal parts of thighs areolate; thoracic fold present, weak. Tongue elliptical, slightly longer than wide, not notched behind, and free posteriorly for about one-fourth of its length; vomerine teeth 3-3, situated on small, widely separated, transverse ridges between rather small elliptical inner nares; no vocal slits.

Color (in alcohol) dark brown with irregular darker reticulations on dorsal surfaces of head, body, and limbs; flanks brown with small creamy white spots; posterior surfaces of thighs dark brown; chin creamy tan; belly grayish brown

with cream-colored flecks; ventral surfaces of limbs pale brown; webbing on feet gray; small white spots in anal region.

Color (in life) chocolate brown with darker brown reticulations and irregular blotches above; flanks brown with yellow spots; belly gray to grayish brown with faint cream-colored spots; iris a deep bronze color.

Variation.—In males the total number of vomerine teeth varies from 4 to 7. In many specimens the vomerine ridges are larger and more closely approximated medially than in the specimen described above. Females attain snout-vent lengths of 51 mm., have as many as 9 vomerine teeth, and have a proportionately larger tympanum than males. Some of the largest specimens of both sexes have indistinct cream-colored pustules scattered on the ventral surface of the forearm. Some individuals have nearly uniform grayish brown ventral surfaces; in others the chin, as well as the abdomen, is brown with cream-colored spots. The dorsal surfaces of some specimens are nearly uniform dark brown with no reticulations. In others the dorsum is paler brown with distinct darker mottling; in some of these there is little mottling laterally, so that there is the effect of an irregular, pale brown, dorsolateral stripe.

Tadpoles.—The tadpoles of this species were described by Rabb and Mosimann (1955). Tadpoles obtained from streams at 3.3 kilometers north and at 8.5 kilometers southeast of Zacualtipán, Hidalgo, are like those described by Rabb and Mosimann in having 2/3 tooth rows, peglike serrations on the beaks, and long rounded tails. The largest tadpole (KU 60078) has small hind legs, a body length of 22 mm., and a total length of 61 mm.

Remarks.—Taylor (1940:393) found frogs of this species in plants along small spring-fed rivulets in an open meadow at El Chico Parque Nacional. Also, he noted that active frogs dove into the streams and took refuge in the mud on the bottom. Rabb and Mosimann (1955:1) found this species along banks of tiny streams in open meadows and noted that the frogs sought refuge in the water. At El Chico Parque Nacional on June 8, 1960, I found *Hyla robertsorum* under rocks along small rivulets by day; at night, when the temperature was 14° C., frogs were sitting on rocks and in junipers overhanging a small stream. At the same locality on June 23 and 24, 1962, frogs of this species were found on rainy nights, when the temperature varied from 10 to 12° C. At this time the frogs were sitting on the grassy banks of rivulets in the meadow. During the day *Hyla robertsorum* was found on the earthen banks of the rivulets in places where dense growths of grass overhung the streams. On December 23, 1959, one specimen of *Hyla robertsorum* was found beneath a rock in a small stream in pine forest at 3.3 kilometers north of Zacualtipán.

Rabb and Mosimann (1955:1) obtained tadpoles of *Hyla robertsorum* from quiet pools of a stream at El Chico Parque Nacional. I found tadpoles in pools in rocky streams in pine forest at 3.3 kilometers north and at 8.5 kilometers southeast of Zacualtipán. Four

completely metamorphosed juveniles obtained on June 8, 1960, at El Chico Parque Nacional have snout-vent lengths of 30.6 to 32.0 mm. Gravid females were found at the same locality on June 8, 1960, and June 23, 1962.

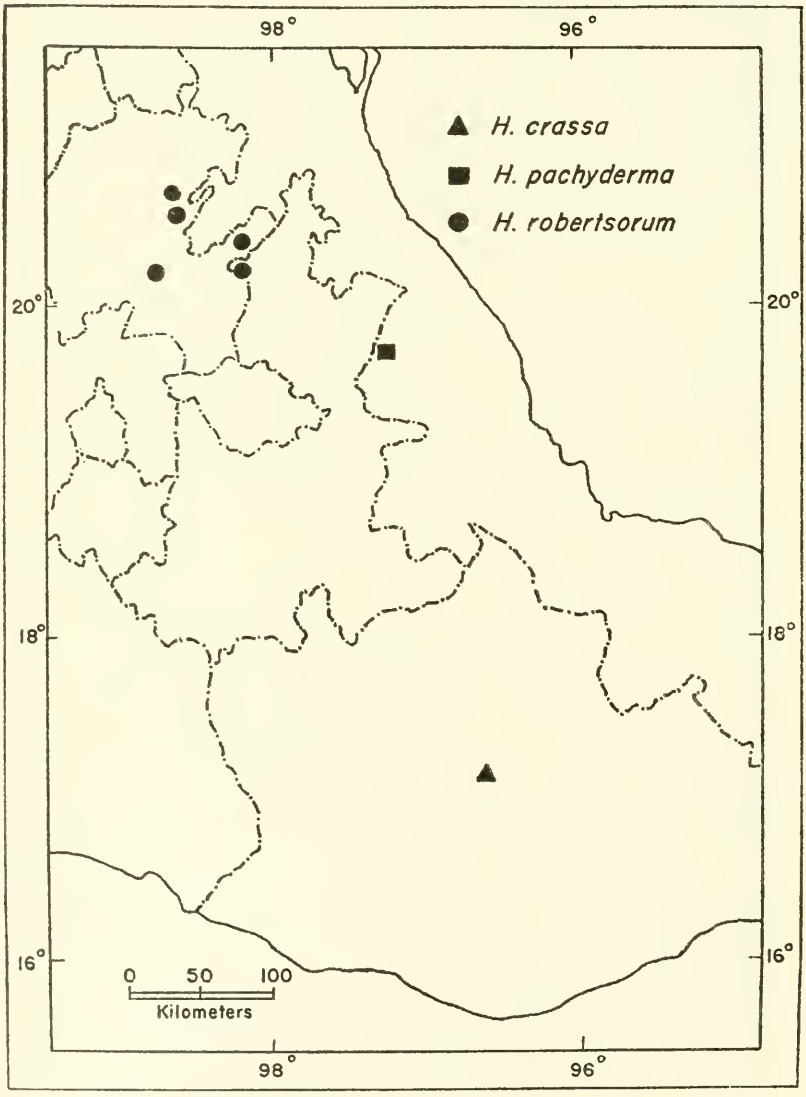


FIG. 4. Map showing locality records for *Hyla crassa*, *Hyla pachyderma*, and *Hyla robertsorum*.

Distribution.—*Hyla robertsorum* inhabits streams in the pine and fir forests in the higher parts (2250 to 3050 meters) of the Sierra Madre Oriental in extreme northern Puebla and eastern Hidalgo (Fig. 4).

Specimens examined.—HIDALGO: 16 km. W Agua Blanca, UMMZ 106432 (6); El Chico Parque Nacional, CNHM 75786, 100124, KU 57650-71, 59824-5 (skeletons), 59914-5 (skeletons), 71269-95, 71757 (skeleton), UIMNH 10349-64, 27022-35, 39434-49, UMMZ 92462, 106401 (5), 106443 (tadpoles), USNM 114762-85, 134268; 3.3 km. N Zacualtipán, KU 53810, 60078 (tadpoles); 8.5 km. SE Zacualtipán, KU 60079 (tadpoles). PUEBLA: Honey, UMMZ 95245.

Hyla pachyderma Taylor

Hyla pachyderma Taylor, Univ. Kansas Sci. Bull., 28:308-310, pl. 27, figs. 1-4, November 12, 1942 [Holotype.—USNM 115029 from Pan de Olla, Veracruz, south of Tezuitlán, Puebla, México; Hobart M. Smith collector]. Taylor and Smith, Proc. U. S. Natl. Mus., 95:588, June 30, 1945. Smith and Taylor, Bull. U. S. Natl. Mus., 194:86, June 17, 1948; Univ. Kansas Sci. Bull., 33:350, March 20, 1950. Rabb and Mosimann, Occ. Papers Mus. Zool. Univ. Michigan, 563:7-8, March 29, 1955.

Diagnosis.—Maximum snout-vent length in males 40 mm.; snout in dorsal profile round; tarsal fold strong; inner metatarsal tubercle round and moderate in size; outer metatarsal tubercle small and indistinct; webbing on foot extending to middle of penultimate phalanx of fourth toe; nuptial spines on thumb large; thoracic fold present; anal opening at level of middle of thighs; dorsum dull grayish brown with scattered indistinct dark flecks; venter cream-color mottled with brown on throat and chest; flanks grayish brown with cream-colored reticulations; anal stripe distinct, creamy white, sometimes extending outward on thighs; white spots or line below anus; vocal slits absent.

Description.—The following description is based on USNM 115028 from Pan de Olla, Veracruz. Adult male having a snout-vent length of 39.9 mm.; tibia length, 21.0 mm., 52.6 per cent of snout-vent length; foot length (measured from proximal edge of inner metatarsal tubercle to tip of longest toe), 20.5 mm.; greatest width of head, 12.8 mm., 32.1 per cent of snout-vent length; head length, 12.3 mm., 30.8 per cent of snout-vent length. Snout short, in lateral profile bluntly rounded, in dorsal profile rounded; canthus rounded; loreal region slightly concave; lips thick, round, and not flaring; nostrils slightly protuberant; internarial distance, 2.7 mm.; interorbital distance, 3.7 mm., somewhat broader than eyelid, 2.9 mm. A heavy dermal fold from posterior corner of eye above tympanic region and then to insertion of forearm; tympanum completely concealed. Forearm moderately robust; distinct fold on wrist; prepollex enlarged bearing cluster of moderate-sized, horny, nuptial spines continuous on edge of digit; row of spines present on second finger; subarticular tubercles round, small proximally and slightly larger distally; supernumerary tubercles small and indistinct; three palmar tubercles, median and outer partly fused; fingers long, moderately slender; discs moderately large; length of fingers from shortest to longest, 1-2-4-3; second and fourth fingers subequal in length; webbing between fingers rudimentary. Heels overlap by about one-fourth length of shank when hind limbs adpressed; tibiotarsal articulation extends to anterior edge of eye; tarsal fold thick, low, extending nearly to heel; inner metatarsal tubercle moderately large and round; outer metatarsal tubercle small and indistinct; subarticular tubercles small and round;

supernumerary tubercles small, present on proximal segments of digits; toes moderately long and slender; length of toes from shortest to longest, 1-2-3-5-4; third and fifth toes subequal in length; toes about three-fourths webbed; web extending to middle of penultimate phalanx of fourth toe; discs rather small, about two-thirds size of those on fingers. Anal opening directed posteroventrally at level of middle of thighs; anal flap slightly elongate; thick, transverse dermal fold above anus. Skin of dorsum and ventral surfaces of limbs, except thighs, smooth; skin of chin, belly, and ventral surfaces of thighs granular; thoracic fold present. Tongue nearly round, slightly notched behind, and barely free posteriorly; vomerine teeth 3-3, situated on posteroventral edges of small, transverse vomerine ridges between rather large triangular inner nares; no vocal slits.

Color (in alcohol) of dorsal surfaces of head, body, and limbs dull grayish brown with indistinct scattered darker flecks; flanks grayish brown with cream-colored reticulations; posterior surfaces of thighs tan; chin cream-color, mottled with brown; belly creamy yellow; anal stripe cream-color.

Variation.—In addition to the specimen described above three others are known. One is a juvenile having a snout-vent length of 29.5 mm., and two are females having snout-vent lengths of 46.9 and 41.6 mm. Variation in structure and coloration between the four specimens is slight. In the females the tympani are partly visible and are about one-third the diameter of the eye; the chest is mottled with brown; the anal stripe extends laterally in the form of a row of cream-colored dashes and spots onto the posterodorsal surfaces of the thighs.

Remarks.—On the basis of the four specimens available for study, *Hyla pachyderma* seems to be closely related to *Hyla crassa* and *Hyla robertsorum.* In the *Hyla bistincta* group, *Hyla pachyderma* is unique in having enlarged nuptial spines.

Taylor and Smith (1945:588) stated that the frogs were found on bushes and weeds beside a small, bounding stream near Pan de Olla. I have searched unsuccessfully for this species in the area around Pan de Olla and Tezuitlán.

Distribution.—This species is known only from a stream at an elevation of about 1600 meters on the Atlantic slopes of the Sierra Madre Oriental in central Veracruz (Fig. 4).

Specimens examined.—VERACRUZ: Pan de Olla, south of Tezuitlán, Puebla, USNM 115026-9.

Hyla crassa (Brocchi)

Cauphias crassus Brocchi, Bull. Soc. Philom. Paris, ser. 7, 1:130, 1877 [Holotype.—MNHN 6331 from "Mexico;" Adolphe Boucard collector].

Cauphias crassum Brocchi, Études des batraciens de l'Amérique Centrale, p. 64, pl. 12, fig. 4, 1882. Díaz de León, Indice de los batracios que se encuentran en la República Mexicana, p. 21, June, 1904. Kellogg, Bull. U. S. Nat. Mus., 160:118-120, March 31, 1932. Taylor, Univ. Kansas Sci. Bull., 26:392, November 15, 1940. Rabb and Mosimann, Occas. Papers Mus. Zool. Univ. Michigan, 563:7, March 29, 1955.

Hyla crassa, Boulenger, Catalogue Batrachia Salientia, 2nd. Ed., p. 396, February 1, 1882. Günther, Biologia Centrali-Americana, Reptilia and Batrachia, p. 281, September, 1901. Nieden, Das Tierreich, Amphibia,

Anura I, p. 248, June, 1923. Smith and Taylor, Bull. U. S. Natl. Mus., 194:86, June 17, 1948. Taylor, Amer. Mus. Novitates, 1437:20, December 7, 1949.

Hypsiboas crassus, Cope, Bull. U. S. Natl. Mus., 32:14, 1887.

Hyla robustofemora Taylor, Univ. Kansas Sci. Bull., 26:389-393, figs. 3-4, November 27, 1940 [Holotype.—UIMNH 25050 (formerly EHT-HMS 16314) from Cerro San Felipe, 15 kilometers northeast of Oaxaca, Oaxaca, México; Edward H. Taylor collector]; Univ. Kansas Sci. Bull., 28:310, November 15, 1942. Smith and Taylor, Bull. U. S. Natl. Mus., 194:86, June 17, 1948. Taylor, Amer. Mus. Novitates, 1437:20, December 7, 1949. Smith and Taylor, Univ. Kansas Sci. Bull., 33:339, March 20, 1950. Rabb and Mosimann, Occas. Papers Mus. Zool. Univ. Michigan, 563:7, March 29, 1955.

Plectrohyla crassa, Hartweg, Occas. Papers Mus. Zool. Univ. Michigan, 437:1, June 30, 1941. Stuart, Occas. Papers Mus. Zool. Univ. Michigan, 455:6, January 5, 1942.

Diagnosis.—Maximum snout-vent length in males 54 mm.; snout in dorsal profile round; tarsal fold strong; inner metatarsal tubercle small and elliptical; outer metatarsal tubercle small, flat, and indistinct; foot fully webbed; nuptial spines on thumb small; thoracic fold absent; anal opening at level of middle of femur; dorsum dull olive-green; belly creamy yellow; chin gray with yellow flecks; flanks dull olive-green with scattered cream-colored spots; and stripe faint, cream-color; vocal slits absent.

Description.—The following description is based on UIMNH 25050 from Cerro San Felipe, Oaxaca. Adult male having a snout-vent length of 53.7 mm.; tibia length, 26.9 mm., 50.1 per cent of snout-vent length; foot length (measured from proximal edge of inner metatarsal tubercle to tip of longest toe), 25.4 mm.; greatest width of head, 17.6 mm., 32.8 per cent of snout-vent length; head length, 16.0 mm., 29.8 per cent of snout-vent length; diameter of eye, 5.4 mm.; diameter of tympanum, 1.5 mm., 27.8 per cent of diameter of eye. Snout short, in lateral profile bluntly rounded, in dorsal profile broadly round; canthus absent; loreal region nearly flat; lips thick and not flaring; nostrils barely protuberant; internarial distance, 3.8 mm.; interorbital distance, 4.7 mm., somewhat broader than width of eyelid, 3.8 mm. Heavy dermal fold from posterior corner of eye above tympanum and then to insertion of forearm; tympanum concealed above, its diameter about equal to its distance from eye. Forearm thick; distinct fold on wrist; prepollex enlarged bearing patch of small nuptial spines continuous on side of digit; similar patch on second finger; subarticular tubercles small and round, none bifid; few supernumerary tubercles on proximal segments of digits; large, flat palmar tubercle; fingers long and slender; length of fingers from shortest to longest, 1-2-4-3; discs moderately large; rudimentary web between second and third fingers and between third and fourth. Legs thick; heels overlap by about one-fourth length of shank when hindlimbs adpressed; tibiotarsal articulation extends to posterior corner of eye; tarsal fold thick, extending to heel; inner metatarsal tubercle small and elliptical; outer metatarsal tubercle small, flat, and indistinct; subarticular tubercles small and round; single row of supernumerary tubercles on proximal segments of each digit; toes moderately short and slender; length of toes from shortest to longest, 1-2-3-5-4; toes fully webbed; flap of skin on inner surface of first toe; discs about same size as those on fingers. Anal opening directed posteroventrally at middle of thighs; anal sheath moderately elongate; small tubercles below anal opening. Skin of dorsum rather smooth, somewhat

granular on dorsal surfaces of limbs; skin of chin and belly moderately granular; that of posterior surfaces of thighs smooth; no thoracic fold. Tongue nearly round, shallowly notched posteriorly, and free for about one-fourth its length; vomerine teeth 5-5, situated on rounded ridges between small inner nares; no vocal slits.

Color (in alcohol) dull olive-green on dorsal surfaces of head, body, and limbs; flanks dull olive-green with scattered cream-colored spots; posterior surfaces of thighs grayish brown with faint creamy mottling; chin gray with cream-colored spots; belly creamy yellow, suffused with gray posteriorly; undersides of feet and webbing gray; anal stripe faint, pale cream-color.

Variation.—The only other known specimen (MNHN 6331) is a female having a snout-vent length of 53.7 mm. and resembling the specimen described above in most details of morphology. In MNHN 6331 the tympanum is completely concealed, and the 8-7 vomerine teeth are arranged in two irregular rows. The female has more cream-colored mottling on the flanks and posterior surfaces of the thighs and more distinct mottling on the throat than the male described above.

Remarks.—The systematic status of *Cauphias crassus* Brocchi has been in doubt since the time of the original description. Brocchi (1877:130) stated: "Les dernieres phalanges sont obtuses, tronqués a leur extrémité antérieure." Brocchi placed the species in his genus *Cauphias* (type species, *C. guatemalensis*), which he considered to be related to *Hylodes* (= *Eleutherodactylus* in the sense used by Brocchi); he thereby placed *Cauphias* in his Hylodidae (= Leptodactylidae, in part). This idea of relationships was perpetuated by Barbour (1927:96), who reported on the second known specimen of *Cauphias guatemalensis* and stated: "When I dissected the sternum I was at once struck by its similarity to Noble's figures of transitional types between arciferal and firmisternal forms. The *Cauphias* sternum recalls some of his figures for *Sminthillus* and *Eleutherodactylus.* This genus is probably most closely related to the latter and has probably become highly modified to meet some peculiar environmental condition or on account of some specialized habits as yet unknown." Kellogg (1932:118) placed *Cauphias* in the Leptodactylidae and stated that the terminal phalanges are T-shaped. Hartweg (1941:1) considered *Plectrohyla* to be the correct generic name for *Cauphias guatemalensis;* he thereby relegated *Cauphias* to the synonomy of *Plectrohyla.* Hartweg (1941:9) further showed that the terminal phalanges of *Plectrohyla guatemalensis* were not T-shaped and that intercalary cartilages were present. Thus, he correctly concluded that *Plectrohyla guatemalensis* (and *P. crassa* by implication) was a member of the family Hylidae. Stuart (1942:6) followed Hartweg's allocations and further suggested that *Plectrohyla crassa* might be the same species as *Hyla*

robustofemora Taylor. In his description of *H. robustofemora* Taylor (1940:392), who had not examined the type of *Cauphias crassus,* stated that were it not for the statements of Brocchi and Kellogg that *C. crassus* has T-shaped terminal phalanges, "I might suspect I had before me a specimen of *Cauphias* closely related to *crassum.*"

I have compared the type of *Cauphias crassus* with that of *Hyla robustofemora.* With the exception of the minor differences mentioned in the preceding section on variation, the specimens are alike, leaving little doubt that they represent the same species. The statements of Brocchi and Kellogg to the contrary, the type of *Cauphias crassus* possesses intercalary cartilages between the penultimate and terminal phalanges; the latter are not T-shaped, but as in the type of *Hyla robustofemora,* resemble those typical of *Hyla.* On the basis of the morphological characters, as pointed out for *Hyla robustofemora* by Taylor (1940:392), *Hyla crassa* is a member of the *Hyla bistincta* group.

Distribution.—This species is definitely known only from a small stream at an elevation of 2300 meters in the mountains of central Oaxaca (Fig. 4).

Specimens examined.—OAXACA: Cerro San Felipe, UIMNH 25050. "Mexico," MNHN 6331.

RELATIONSHIPS

The evolutionary trend in the members of the *Hyla bistincta* group is towards aquatic habits. *Hyla bistincta,* the least specialized species in the group, has relatively short fingers, webbing between the fingers, a truncate, high snout, and relatively large subarticular and supernumerary tubercles. *Hyla charadricola* resembles *bistincta* in having relatively short fingers, a slight amount of webbing, and a truncate snout. Apparently these two species are more closely related to one another than either is to the other species in the group. *Hyla robertsorum, pachyderma,* and *crassa* are the most aquatic members of the group. These species are closely related, possibly conspecific. All have round, sloping snouts, robust forearms, long, unwebbed fingers, and large webbed feet. Both *H. pachyderma* and *H. crassa* seem to be advanced beyond *H. robertsorum.* If small nuptial spines, moderately webbed feet, and absence of a well-defined thoracic fold are considered to be less advanced than large nuptial spines and a strong thoracic fold, as in *H. pachyderma,* or fully webbed feet, as in *H. crassa,* then *H. robertsorum* must be considered to be less advanced than *H. pachyderma* or *H. crassa.*

Members of the *Hyla bistincta* group inhabit mountain streams.

The frogs can be found along these streams throughout the year. Since in most stream-breeding hylids there is no migration to breeding sites, the breeding call does not function to attract females to the breeding site. Apparently voices are lacking in all members of the *Hyla bistincta* group, except in *Hyla bistincta.* The presence of vocal slits and the ability to call further indicate that *Hyla bistincta* is the primitive member of this group.

Members of the *Hyla bistincta* group and the species of *Plectrohyla* closely resemble each other in osteology and body form of the adults and in structure of the tadpoles. This resemblance suggests a close relationship between the two groups. *Plectrohyla* apparently evolved from an ancestral stock resembling the extant *Hyla bistincta.* Probably this stock gave rise independently to *Plectrohyla* and to the *Hyla robertsorum-pachyderma-crassa* complex. In the former the voice was retained, and a projecting prepollex spine developed, whereas in the latter the voice was lost, and the prepollex spine did not project. *Plectrohyla* lives in mountain streams in the Chiapan-Guatemalan highlands; the *Hyla robertsorum-pachyderma-crassa* complex inhabits similar environments in the Sierra Madre Oriental in México. *Hyla charadricola* also lives in the Sierra Madre Oriental, whereas *Hyla bistincta* is widespread in the mountains of México southeastward to the Isthmus of Tehuantepec.

LITERATURE CITED

BARBOUR, T.
1927. *Cauphias* rediscovered. Copeia, no. 165:96-98, December 23.

BROCCHI, P.
1877. Note sur quelques batraciens hylaeformes recueillis au Mexique et au Guatemala. Bull. Soc. Philom. Paris, ser. 7, 1 (3):122-132.

DUELLMAN, W. E.
1961. The amphibians and reptiles of Michoacán, México. Univ. Kansas Publ. Mus. Nat. Hist., 15:1-148, pls. 1-6, December 20.

HARTWEG, N.
1941. Notes on the genus *Plectrohyla*, with descriptions of new species. Occas. Papers Mus. Zool. Univ. Michigan, 437:1-10, pl. 1, June 30.

KELLOGG, R.
1932. Mexican tailless amphibians in the United States National Museum. Bull. U. S. Natl. Mus., 160:iv + 224 pp., pl. 1, March 31.

RABB, G. B. and MOSIMANN, J. E.
1955. The tadpole of *Hyla robertsorum*, with comments on the affinities of the species. Occas. Papers Mus. Zool. Univ. Michigan, 563:1-9, March 29.

SHANNON, F. A.
1951. Notes on a herpetological collection from Oaxaca and other localities in Mexico. Proc. U. S. Natl. Mus., 101:465-484, May 17.

STUART, L. C.
1942. Descriptions of two new species of *Plectrohyla* Brocchi, with comments on several forms of tadpoles. Occas. Papers Mus. Zool. Univ. Michigan, 455:1-14, January 5.

TAYLOR, E. H.
1940. New species of Mexican Anura. Univ. Kansas Sci. Bull., 41:385-405, November 27.
1948. A new hylid frog from eastern Mexico. Univ. Kansas Publ. Mus. Nat. Hist., 1:259-262, August 16.
1949. A new hylid frog from central Veracruz. Copeia, 1949 (4):272-274, pl. 1, December 15.

TAYLOR, E. H. and SMITH, H. M.
1945. Summary of the collections of amphibians made in México under the Walter Rathbone Bacon Traveling Scholarship. Proc. U. S. Natl. Mus., 95:521-613, pls. 18-32, June 30.

Transmitted June 24, 1963.

29-8590

S - NH - Lawrence

University of Kansas Publications
Museum of Natural History

Volume 15, No. 10, pp. 493-564, pls. 23-25, 14 figs.
May 17, 1965

MUS. COM. ZOOL
LIBRARY
DEC 31 1965
HARVARD
UNIVERSITY

An Ecological Study of the Garter Snake, Thamnophis sirtalis

BY

HENRY S. FITCH

University of Kansas
Lawrence
1965

UNIVERSITY OF KANSAS PUBLICATIONS
MUSEUM OF NATURAL HISTORY

Institutional libraries interested in publications exchange may obtain this series by addressing the Exchange Librarian, University of Kansas Library, Lawrence, Kansas. Copies for individuals, persons working in a particular field of study, may be obtained by addressing instead the Museum of Natural History, University of Kansas, Lawrence, Kansas. There is no provision for sale of this series by the University Library, which meets institutional requests, or by the Museum of Natural History, which meets the requests of individuals. Nevertheless, when individuals request copies from the Museum, 25 cents should be included, for each separate number that is 100 pages or more in length, for the purpose of defraying the costs of wrapping and mailing.

° An asterisk designates those numbers of which the Museum's supply (not the Library's supply) is exhausted. Numbers published to date, in this series, are as follows:

Vol. 1. Nos. 1-26 and index. Pp. 1-638, 1946-1950.

°Vol. 2. (Complete) Mammals of Washington. By Walter W. Dalquest. Pp. 1-444, 140 figures in text.

Vol. 3. Nos. 1-4 and index. Pp. 1-681. 1951.

°Vol. 4. (Complete) American weasels. By E. Raymond Hall. Pp. 1-466, 41 plates, 31 figures in text. December 27, 1951.

Vol. 5. Nos. 1-37 and index. Pp. 1-676, 1951-1953.

°Vol. 6. (Complete) Mammals of Utah, *taxonomy and distribution*. By Stephen D. Durrant. Pp. 1-549, 91 figures in text, 30 tables. August 10, 1952.

Vol. 7. Nos. 1-15 and index. Pp. 1-651, 1952-1955.

Vol. 8. Nos. 1-10 and index. Pp. 1-675, 1954-1956.

Vol. 9. Nos. 1-23 and index. Pp. 1-690, 1955-1960.

Vol. 10. 1. Studies of birds killed in nocturnal migration. By Harrison B. Tordoff and Robert M. Mengel. Pp. 1-44, 6 figures in text, 2 tables. September 12, 1956.

2. Comparative breeding behavior of Ammospiza caudacuta and A. maritima. By Glen E. Woolfenden. Pp. 45-75, 6 plates, 1 figure. December 20, 1956.

3. The forest habitat of the University of Kansas Natural History Reservation. By Henry S. Fitch and Ronald R. McGregor. Pp. 77-127, 2 plates, 7 figures in text, 4 tables. December 31, 1956.

4. Aspects of reproduction and development in the prairie vole (Microtus ochrogaster). By Henry S. Fitch. Pp. 129-161, 8 figures in text, 4 tables. December 19, 1957.

5. Birds found on the Arctic slope of northern Alaska. By James W. Bee. Pp. 163-211, plates 9-10, 1 figure in text. March 12, 1958.

°6. The wood rats of Colorado: distribution and ecology. By Robert B. Finley, Jr. Pp. 213-552, 34 plates, 8 figures in text, 35 tables. November 7, 1958.

7. Home ranges and movements of the eastern cottontail in Kansas. By Donald W. Janes. Pp. 553-572, 4 plates, 3 figures in text. May 4, 1959.

8. Natural history of the salamander, Aneides hardyi. By Richard F. Johnston and Gerhard A. Schad. Pp. 573-585. October 8, 1959.

9. A new subspecies of lizard, Cnemidophorus sacki, from Michoacán, México. By William E. Duellman. Pp. 587-598, 2 figures in text. May 2, 1960.

10. A taxonomic study of the middle American snake, Pituophis deppei. By William E. Duellman. Pp. 599-610, 1 plate, 1 figure in text. May 2, 1960.

Index. Pp. 611-626.

Vol. 11. Nos. 1-10 and index. Pp. 1-703, 1958-1960.

Vol. 12. 1. Functional morphology of three bats: Eumops, Myotis, Macrotus. By Terry A. Vaughan. Pp. 1-153, 4 plates, 24 figures in text. July 8, 1959.

°2. The ancestry of modern Amphibia: a review of the evidence. By Theodore H. Eaton, Jr. Pp. 155-180, 10 figures in text. July 10, 1959.

3. The baculum in microtine rodents. By Sydney Anderson. Pp. 181-216, 49 figures in text. February 19, 1960.

°4. A new order of fishlike Amphibia from the Pennsylvanian of Kansas. By Theodore H. Eaton, Jr., and Peggy Lou Stewart. Pp. 217-240, 12 figures in text. May 2, 1960.

5. Natural history of the bell vireo. By Jon C. Barlow. Pp. 241-296, 6 figures in text. March 7, 1962.

6. Two new pelycosaurs from the lower Permian of Oklahoma. By Richard C. Fox. Pp. 297-307, 6 figures in text. May 21, 1962.

7. Vertebrates from the barrier island of Tamaulipas, México. By Robert K. Selander, Richard F. Johnston, B. J. Wilks, and Gerald G. Raun. Pp. 309-345, plates 5-8. June 18, 1962.

8. Teeth of Edestid sharks. By Theodore H. Eaton, Jr. Pp. 347-362, 10 figures in text. October 1, 1962.

(Continued on inside of back cover)

University of Kansas Publications
Museum of Natural History

Volume 15, No. 10, pp. 493-564, pls. 23-25, 14 figs.
May 17, 1965

An Ecological Study of the Garter Snake, Thamnophis sirtalis

BY

HENRY S. FITCH

University of Kansas
Lawrence
1965

S - NA - [Lawrence]

University of Kansas Publications, Museum of Natural History

Editors: E. Raymond Hall, Chairman, Henry S. Fitch,
Theodore H. Eaton, Jr.

Volume 15, No. 10, pp. 493-564, pls. 23-25, 14 figs.
Published May 17, 1965

MUS. COM... OOL
LIBRARY
DEC 31 ...
HARVARD
UNIVERSITY

University of Kansas
Lawrence, Kansas

PRINTED BY
HARRY (BUD) TIMBERLAKE, STATE PRINTER
TOPEKA, KANSAS
1965
30-3965

An Ecological Study of the Garter Snake, Thamnophis sirtalis

BY

HENRY S. FITCH

CONTENTS

PAGE

INTRODUCTION 495
DESCRIPTION 497
GEOGRAPHIC VARIATION 501
HABITAT 505
TEMPERATURE RELATIONSHIPS 508
FOOD HABITS 513
BREEDING 518
Number of young in brood 521
Timing of breeding cycle 526
GROWTH 527
MOVEMENTS 536
DEFENSE AND ESCAPE 540
NATURAL ENEMIES 544
PARASITES 546
COMPOSITION OF THE POPULATION 548
NUMBERS 551
SUMMARY 555
LITERATURE CITED 560

INTRODUCTION

Over much of North America the most abundant and conspicuous species of snake is the garter snake, *Thamnophis sirtalis*. It attains remarkably high population densities and obviously it figures significantly in the economy of local ecosystems. Hence, it has important economic bearing. Occasionally it preys upon pest species,

but the bulk of its predation is upon earthworms and amphibians that certainly are not harmful to man's interest and sometimes are highly beneficial to agriculture. The present account does not attempt to offer a final judgment as to the species' economic role; obviously this varies according to the time and place. In my study no corroboratory evidence could be obtained of the oft-repeated statement that garter snakes feed on insects.

Over the past 30 years I have collected and studied this garter snake in most of the states in the western half of the United States. From 1948 through 1963 I studied a local population on the University of Kansas Natural History Reservation. In 1959 this study was intensified and extended to the adjacent Rockefeller Tract (hereinafter meant to be included whenever the Reservation is mentioned), while concurrently similar field work was carried on at Harvey County Park, some 140 miles southwest of the Reservation.

This field study of the garter snake was based primarily upon live-trapping. The traps used were wire cylinders of quarter-inch mesh, with entrance funnels having inward-projecting wire prongs. The first-year snakes were small enough to pass easily through the quarter-inch mesh; hence they were poorly represented in the catch. Traps of finer mesh were tested but were on the whole unsatisfactory because the more flexible wire permitted ingress of predators more readily, and because a variety of arthropods, some of kinds harmful to the snakes, were caught with them.

By November 5, 1963, 1097 individual garter snakes had been captured a total of 1354 times on the Reservation, and 661 snakes of this species had been captured 812 times at Harvey County Park and neighboring areas. My conclusions are based primarily on the records of the recaptured snakes, for which growth, movement, and other information was available. However, it was not possible to achieve a marked population, and even in the later stages of the study the majority of records pertained to new individuals caught for the first time. For the last six years of the study at the Reservation, the percentages of recapture records were as follows: 1958—19 per cent; 1959—27 per cent; 1960—27 per cent; 1961—27 per cent; 1962—21 per cent; 1963—26 per cent. The rapid population turnover from year to year prevented obtaining a higher percentage of marked individuals.

At the Reservation *T. sirtalis* was the only kind of garter snake present; although the locality is within the ranges of both *T. radix* and *T. proximus*, both are rare locally. On the Harvey County

study area *T. radix* also was present, but in relatively small numbers, and the findings concerning it have not been incorporated in the present report.

The study of *Thamnophis sirtalis* herein reported upon was one phase of an ecological and life history study of Kansas snakes, which was supported by three successive grants from the National Science Foundation (G-3413, G-6158, G-16104) from 1957 through 1962. Many persons helped in various ways with the field work. In almost all instances these were the same individuals whose assistance has already been acknowledged in earlier papers concerning snakes of the Reservation (Fitch, 1960:92; 1963b:357). Mr. Dwight R. Platt is due special credit for his supervision of the field work at Harvey County Park, and active participation in it in 1959 through 1963. Mr. Richard S. Funk helped with the maintenance and study of a colony of captive garter snakes in the winter of 1963 and 1964. Dr. William R. Murchie kindly identified several earthworms. Dr. William H. Coil and Mr. Willis A. Reid kindly identified flukes found in the mouths of garter snakes in 1963 and provided information concerning them. My wife, Virginia R. Fitch, read the manuscript critically and helped me in various other ways. My son, John H. Fitch, assisted me with the photography of living garter snakes.

DESCRIPTION

The scalation is that of a typical colubrid. The body scales are in 19 rows, of which those in the lowest row on each side are broadly oval and smooth or only weakly keeled, whereas those of the remaining rows are narrower and strongly keeled. At a point a little more than 61 per cent of the distance from the snout to the vent the scales of the fourth row on each side abruptly become smaller and then disappear altogether. Immediately beyond the point where the fourth row disappears scales of the adjacent third and fifth rows are somewhat enlarged to occupy the space of the missing fourth row. The remaining 17 rows extend to the posterior end of the body, but drop out in rapid succession on the tail.

The cephalic scutellation is typical of colubrids in general, of natricines, and of the genus *Thamnophis* (Plate 23, fig. 1). The rostral plate is large and prominent. The scutes of the top of the head are: the internasals, the prefrontals, the frontal (bordered on each side by a supraocular), and the paired parietals. The naris is situated between two nasals, near their upper edge. The posterior nasal is somewhat larger than the anterior. The loreal is relatively large. The eye is bordered anteriorly by a preocular and behind usually by three (sometimes only two) small postoculars, which decrease in size from the uppermost to the lowest. There is a single anterior temporal between the

parietal (above) and the fifth and sixth supralabials (below). Behind the anterior temporal there are usually two posterior temporals, one above the other, but the number may be increased to three or reduced to one. There are seven supralabials, increasing progressively in size from the anteriormost to the fifth then decreasing again. The third and fourth are in contact with the lower edge of the eye. The second supralabial is relatively elongate and is the homologue of both the second and the third in the many kinds of garter snakes that have eight pairs of supralabials. There are most often 10 pairs of infralabials. The first pair of infralabials is small but the second pair is even smaller. From the second to the fifth there is progressive increase in size and from the fifth to the tenth there is progressive decrease. The genials are in two pairs, anterior and posterior. Those of the posterior pair are markedly longer (usually from 20 to 40 per cent). The anal plate is undivided. The subcaudals are normally in two series—left and right—alternately placed. Each subcaudal is broadly hexagonal.

The body scales are notched at the tip. In the adult male, scales of the chin region, the anterior genials and several anterior pairs of infralabials, have sensory pits which function during courtship, as the male presses his chin against the female's back. Also, in the adult male, several scales near the anal plate on each side have their keels especially heavy, with knobs developed on them. These knobbed keels likewise function in courtship.

The color pattern is, of course, subject to much geographic variation over the range as a whole. In some localities it is remarkably stable but in others including those of my study areas, it is subject to a wide range of individual variation. The dorsal stripe is the most prominent feature of the pattern. It begins on the nape and extends for the full length of the body and tail, occupying the mid-dorsal scale row, and half (or a little more) of each adjacent row. It is buffy yellow, contrasting with the dark dorsolateral area on each side. These dorsolateral areas are almost black in some individuals but in others dark brown or olive, sufficiently pale so that a pattern of two alternating rows of black spots is faintly discernible. Also, there are much paler areas, which are confined chiefly to the skin between the scales, hence scarcely noticeable except when the skin is stretched. These marks are much more prominent on the lower part of each dorsolateral area, and they become smaller farther dorsally. The marks tend to be bluntly crescent-shaped, but the bulge of one crescent may contact that of the crescent above or below it, the two forming an H-shaped mark. In about ten per cent of the snakes examined, the pale markings were all yellowish or faintly suffused with bluish or greenish, but in most of the snakes at least the lower markings—those between rows 3 and 4, 4 and 5, and 5 and 6—were red, salmon, pink, or rusty. The less prominent marks between rows 6 and 7, 7 and 8, and 8 and 9 usually do not have well-defined reddish suffusion, and if they do, it is paler and more diffuse than in the lower markings. The lateral stripe occupies approximately the upper half of the second scale row and the lower half of the third. It is dull yellow, suffused with dusky pigment, and lacks well-defined borders, blending into the duskier areas above and below it. Below the lateral stripe, a darker area, partly suffused with dusky pigment, and also having scattered black spots, includes the lower half of the second scale row, all of the first row, and the adjacent tips of the ventral scutes. The ventral surface is white in the chin

region, but becomes increasingly grayish farther posteriorly, with a faint suffusion of greenish blue.

In occasional individuals with erythristic tendencies, the red markings on the lower part of the dorsolateral area blend into the lateral stripe suffusing it with reddish, although it has no well defined markings. Reddish suffusion may even extend to the edge of the ventral surface. In broods of garter snakes that were born in captivity, the red lateral markings were much duller than in the mothers and were reddish tan or dull rusty, remarkably uniform among the members of a brood. Seemingly, the brighter, adult coloration is acquired early in development, well before sexual maturity. There is no noticeable difference between the sexes, nor between adults and partly grown individuals, either in pattern or in intensity of color.

There is little evidence of geographic variation in size in *Thamnophis sirtalis*, but as yet no investigation has been made to determine whether such variation exists. Table 1 shows snout-vent lengths and weights of individuals of various categories.

Because of allometric growth and slight sexual dimorphism, individual garter snakes, even from the same locality, differ considerably in proportions. Some of the most striking differences involve the proportions of the head, and the relative size of the head as compared with the body. The changes are gradual, but for the purpose of discussion four arbitrary ontogenetic stages may be recognized. First, in the late embryo, as figured by Zehr (1962:326 and 327) the head is relatively enormous and is bent at right angles to the body, the forehead bulges, and the eyes are remarkably large and protruding; second, in the newborn young the head is aligned with the body but is still relatively large causing the eyes to be conspicuous in profile in dorsal view, the rostrum is fully as wide as the posterior part of the head, and the head is conspicuously wider than any part of the body; third, in partly grown individuals or small adults, the head is conspicuously wider than the neck but not so wide as the

TABLE 1.—SIZES OF THAMNOPHIS SIRTALIS PARIETALIS FROM RESERVATION AND HARVEY COUNTY PARK

	Adult females		Adult males		Newborn young	
	Snout-vent (millimeters)	Weight (grams)	Snout-vent (millimeters)	Weight (grams)	Snout-vent (millimeters)	Weight (grams)
Maximum.....	950	410	678	110	191	2.5
Average (or typical)*	550	57	455	31.5	168	1.9
Minimum.....	504	21	387	14	134	.71

* For adult males and adult females the "typical" size shown is for two-year-olds, since these make up the most numerous size groups.

TABLE 2.—TAIL-LENGTH AS A PERCENTAGE OF SNOUT-VENT LENGTH IN MALE AND FEMALE THAMNOPHIS SIRTALIS PARIETALIS OF DIFFERENT SIZE GROUPS (FROM RESERVATION)

Tail-length: percentage of snout-vent length	Size group: snout-vent length									
	Up to 200 mm.		201 to 400 mm.		401 to 600 mm.		601 to 800 mm.		More than 800 mm.	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
24	..	..	..	..	..	1	..	1	..	..
25	..	..	..	..	..	4	..	4	..	1
26	..	..	..	..	..	10	..	9	..	4
27	..	2	..	4	1	25	..	40	..	3
28	..	6	..	4	5	44	1	34	..	2
29	4	7	2	5	8	45	..	28	..	2
30	4	11	2	8	17	46	2	14	..	1
31	11	18	2	7	36	21	3	10	..	1
32	20	10	3	5	38	16	3	3	..	1
33	19	4	11	6	67	3	2	1	..	..
34	11	1	6	3	52	4	1	..	..	..
35	6	..	1	..	38	..	1	..	..	..
36	1	..	3	..	25	..	..	..	..	..
37	..	..	1	..	9	..	..	..	..	..

widest part of the body, the eyes, though large as compared with those of most other kinds of snakes, are only slightly noticeable in profile from dorsal view, and the proportions of the head are "normal"; fourth, in old adult females, which attain by far the largest size, and in which allometric growth progresses farthest, the eye is relatively small, and does not appear in profile from dorsal view at all, or is not prominent, the temporal segment of the head is relatively wide as compared with the rostral portion causing the head to appear to be triangular, the neck is thick, and the body is stout.

In newborn males the tail averages approximately one-third of the snout-vent length, whereas it is approximately 31 per cent of the snout-vent length in newborn females. In adult males the relative length of the tail has changed slightly if at all, still averaging about one-third of the snout-vent length, whereas in females of corresponding size (400 to 600 millimeters) the tail averages only about 29 per cent of snout-vent length, and in larger females (more than 600 millimeters) it averages only a little more than 27 per cent. Large old females thus deviate from the bodily proportions of juveniles much more markedly than do other individuals (see Table 2).

In Table 1 the snout-vent lengths and weights given as maximum (and those given as minimum) do not necessarily represent the same individual. For each length there is a wide range of variation in weights, and as length increases, the variability increases. Females are more variable than males, also, they attain greater lengths, and their weights are subject to more fluctuation being unusually high when the snakes are gravid and unusually low after parturition. The graph in Figure 1 shows correlation of weight with length in male and female garter snakes all from the Reservation and Rockefeller Tract.

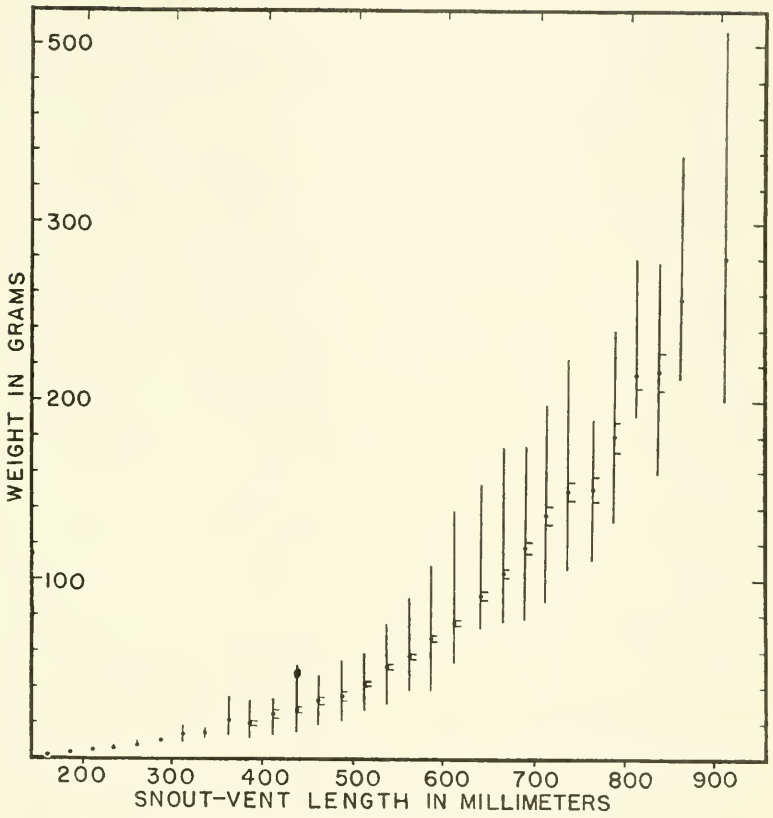


FIG. 1. Diagram showing correlation of weight with snout-vent length in live garter snakes on the Reservation. For each sample of 25-millimeter range in snout-vent length, the mean, minimum and maximum weights are shown. Standard error of the mean is shown for each series having a sufficient number of individuals. Males and females are combined in the samples shown here. The trends of correlation in length and weight are alike for the sexes, except that adult females tend to vary more in weight and, in early summer, to be slightly heavier than adult males of the same length, because of their developing embryos.

GEOGRAPHIC VARIATION

Thamnophis sirtalis is a polytypic species with an enormous geographic range (Fig. 2) which exceeds in area that of any other North American snake, extending from coast to coast and from the northernmost limits of areas habitable by snakes in the western hemisphere south to subtropical regions. The species as a whole has not been the subject of taxonomic revision since Ruthven's

(1908) classic but much outdated monograph of the genus *Thamnophis.* Eleven subspecies are currently recognized. Some of these are rather weakly differentiated, yet probably still others worthy of recognition would be discerned if all geographic populations were subjected to careful scrutiny. Among North American species of snakes only the *Thamnophis elegans, Diadophis punctatus,* and *Lampropeltis doliata* complexes exceed *Thamnophis sirtalis* in amount of racial differentiation, but in the first two of these some of the forms have become differentiated beyond the subspecific level and genetically isolated.

Thamnophis sirtalis sirtalis is the best known subspecies and ranges over an extensive area, from New York and Florida west to Minnesota and Louisiana, with a considerable amount of variation, both individual and local. The dorsal stripe typically is yellow, well developed but with edges not sharply defined, and with dark spots encroaching. There are lateral stripes, less well defined than the dorsal, and the dorsolateral areas on each side are dark but with even darker areas in two alternating rows of spots. The numbers of ventrals and subcaudals are relatively low as compared with those in most of the other subspecies. Some of the northern populations have a tendency to melanism. *T. s. pallidula* is a northeastern race occurring entirely within recently glaciated regions in Maine, New Hampshire, Vermont, northern New York, and neighboring regions of southeastern Canada. In this subspecies the dorsal stripe is either completely lacking or is dull colored, grayish, and indistinct. Dorsolateral dark spots are conspicuous. Ventrals and subcaudals both average approximately seven or eight fewer than in neighboring populations of *T. s. sirtalis.*

T. s. semifasciata is a localized subspecies occurring in typical form only on or near the shores of Lake Michigan in the Chicago region. It differs from *T. s. sirtalis* which presumably is its parent subspecies in having the lateral stripes broken by a series of dark transverse markings.

T. s. parietalis is the subspecies of the Great Plains. It differs from typical *sirtalis* in having from eight to ten more ventrals and subcaudals (when individuals of the same sex are compared), but more especially in having the pale flecks of the dorsolateral area red, salmon, or orange, rather than yellow, bluish or greenish as in typical *sirtalis.* The transition from the pale flecks of *sirtalis* to the red flecks of *parietalis* is extremely gradual and intermediates or mixed populations occur from Michigan and Ohio to Minnesota

and Kansas. *T. s. parietalis* differs from the West Coast subspecies in having semicircular black spots on the edges of the ventrals. *T. s. annectens* replaces *parietalis* to the south of the latter's range, in Oklahoma and Texas. In *annectens* the dorsal stripe is bright orange instead of yellow, and the dorsolateral flecks are pale as in *T. s. sirtalis*. *T. s. ornatus,* an isolated subspecies, inhabits the Rio Grande drainage of south-central Colorado, New Mexico and north-central Mexico and resembles *parietalis* in most respects, but has a relatively pale, grayish brown dorsolateral area.

West of the Rocky Mountains in the Great Basin region and the eastern parts of Pacific states and provinces another subspecies, *T. s. fitchi,* occurs from Alaska and northern British Columbia to southern California. It resembles *parietalis* most closely but differs in lacking black lateral spots on the ventrals and in having brighter, scarlet marks which are limited to the lower half of the dorsolateral area on each side. In this latter respect it resembles all the West Coast subspecies. The subspecies *T. s. pickeringi* in northwestern Washington has melanistic tendencies; its dorsal stripe is narrowed and limited to the middorsal scale row, the lateral stripes are partly or entirely obscured, and the ventral surface is heavily clouded with black pigment. *T. s. concinnus* of the Williamette Valley in northwestern Oregon is another melanistic subspecies having the lateral stripes partly or entirely obscured, but it differs from *pickeringi* in having the dorsal stripe of normal width (involving not only the middorsal scale row but half of the row adjacent on each side), and in having the head bright red rather than dark olive as in most other subspecies. *T. s. concinnus* and *T. s. pickeringi* are alike in having relatively low numbers of ventrals and subcaudals. *T. s. infernalis* occupies a narrow coastal strip for most of the length of California. It resembles *fitchi* in most respects but has on the average a much paler dorsolateral area (gray rather than black) and on the average fewer ventrals and subcaudals. *T. s. tetrataenia* is another coastal subspecies, but is localized in a relatively small area—the San Francisco peninsula. It is perhaps the most distinctive of all the subspecies. Like *concinnus* it has a red head but lacks melanistic tendencies and instead has the red marks on the sides enlarged, and extended longitudinally forming bands running for the whole length of the body.

Numbers of ventrals and subcaudals are subject to much geographic variation over the range as a whole, but in the western three-fourths of the species' range at least their changes do not

correspond accurately with the subspecific boundaries outlined above. Instead, there are clines with lowest numbers of these scales in the population situated farthest north or along the coast, and highest numbers in populations living farther interiorly or farther south. In most taxonomic studies of garter snakes these meristic characters have been heavily relied upon, but experimental work by Fox (1948) has demonstrated that the differences between individuals and populations are not necessarily genetic. The temperature at critical stages of embryonic development (in *Thamnophis elegans*) was found by Fox to affect the numbers of scales. In view of these findings it seems best to de-emphasize numbers of ventral and subcaudal scales and concentrate attention on differences in color and pattern in defining geographic races.

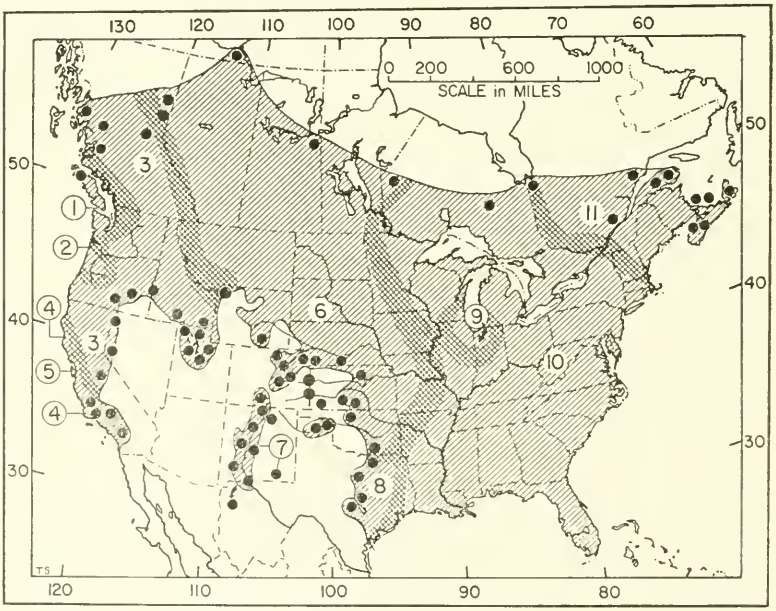


FIG. 2. Geographic range of *Thamnophis sirtalis* (shaded) with marginal or near-marginal records of occurrence (dots). More heavily shaded areas show known or presumed intergradation between subspecies: 1. *T. s. pickeringi*, 2. *T. s. concinnus*, 3. *T. s. fitchi*, 4. *T. s. infernalis*, 5. *T. s. tetrataenia*, 6. *T. s. parietalis*, 7. *T. s. ornata*, 8. *T. s. annectens*, 9. *T. s. semifasciata*, 10. *T. s. sirtalis*, 11. *T. s. pallidula*. Many disjunct populations occur in the southwestern part of the range. The same statement probably applies also in the northern part, but as yet the distribution in Canada is poorly known. Probably the ranges of *T. s. parietalis* and *T. s. fitchi* are to a large extent separated by uninhabitable areas along the Continental Divide. This map is based on information from Fitch (1941:576), Stebbins (1954:505), Logier and Toner (1961:69 and 71), Fitch and Maslin (1961:296), and Smith (1961:223).

HABITAT

Thamnophis sirtalis parietalis prefers a habitat of mesic vegetation. On the Reservation these garter snakes were caught in every habitat where traps were set, but the mixture of diverse habitats in juxtaposition probably often resulted in their wandering into situations different from those they preferred. Judging from the relative numbers caught in different situations, some of the major habitats of my study areas ranked as follows in order of preference.

1. Margins of ponds (Plate 24, fig. 1), with rank low vegetation such as smartweed (*Polygonum* sp.), barnyard grass (*Echinochloa crus-galli*), and giant ragweed (*Ambrosia trifida*). In dry weather there was often a zone of dried mud several feet or several yards wide between the water level and the zone of rank vegetation. Garter snakes were often found in this barren zone hiding beneath boards or beneath a small rowboat beached there.

2. Silt flat about an acre in extent at upper end of Reservation Pond beneath an open grove of willows and other trees, and having a thick ground vegetation of dayflower (*Commelina communis*), rice cutgrass (*Leersia oryzoides*) and others.

3. Woodland edge, and isolated thickets of crab apple (*Pyrus ioensis*), plum (*Prunus americanus*), dogwood (*Cornus drummondi*), sumac (*Rhus glabra*), and elm (*Ulmus americana*) in prairie or pastureland.

4. Prairie with native tall-grasses, including bluestems (*Andropogon gerardi* and *A. scoparius*), switchgrass (*Panicum virgatum*) and Indian grass (*Sorghastrum nutans*) (Plate 24, fig. 2).

5. Meadow with introduced pasture grasses, especially awnless brome (*Bromus inermis*) and blue-grass (*Poa pratensis*).

6. Fallow field in bottomland, with rank growth of giant ragweed and sunflower (*Helianthus annuus*).

7. Woodland with elm, oak (*Quercus muhlenbergii, Q. velutina, Q. borealis*), hickory (*Hicoria ovata*), ash (*Fraxinus americanus*), honey locust (*Gleditsia triacanthos*), osage orange (*Maclura pomifera*), Kentucky coffee tree (*Gymnocladus dioica*), redbud (*Cercis canadensis*) and dogwood.

8. Upland fallow field with sparse weedy vegetation, three-awned grass (*Aristida oligantha*), common lespedeza (*Lespedeza striata*) and, at a later stage of succession, asters (*Aster* sp.) and goldenrods (*Solidago* sp.)

9. Disturbed and relatively barren situations such as gravel roads, rock quarry, yards and lawns.

This listing of habitats applies primarily to garter snakes in their summer ranges. In autumn they were most often caught along hilltop limestone outcrops in woodland, situations rarely frequented in summer. Obviously they had repaired to the outcrops to hibernate. Probably some made the trip after forest trees had shed their leaves and the aspect of the forest was much altered from that prevailing in summer.

The more moist the situation, the more favorable it seems to be

for the garter snake. In dry weather, especially, the two ponds on my main study area seemed to be especially favored locations, but there was little tendency for the snakes to concentrate about them. Instead, the snakes remained scattered over the entire area, in a variety of habitats. This lack of concentration is somewhat surprising because several of the main prey species on the area, especially the leopard frog, do tend to remain concentrated near the ponds and streams at most times and disperse to other habitats only in wet weather.

Smith (1956:292-293) wrote of *Thamnophis sirtalis* in Kansas ". . . one of the most ubiquitous snakes . . . It does not appear to be confined in particular to aquatic habitats, although it occurs there in perhaps greater abundance than elsewhere. It is the common garter snake in towns, where it may be found in vacant lots and overgrown yards." However, farther west in the central part of Kansas this garter snake becomes increasingly rare and localized and limited to aquatic situations as woodlands give way to grasslands, and mesic vegetation becomes scarce.

The subspecies of the Pacific Coast states and Great Basin are less likely to be found wandering far from water than is *parietalis*. In this far western part of its range *sirtalis* ". . . is primarily a swamp snake, and is most abundant on low wet ground where there is dense vegetation. Along the margins of sloughs, along slow-moving watercourses, and in lush meadows along small coastal streams, it occurs in abundance . . ."; ". . . pre-eminently a marsh- or meadow-inhabiting species. Everywhere that it occurs it seems to favor a habitat of thick vegetation in damp places . . ." (Fitch, 1941a:8; 1941b:590).

Wright and Wright (1957:837) have reviewed an extensive literature concerning the habitat of *T. sirtalis* in eastern North America (chiefly pertaining to the subspecies *T. s. sirtalis* but including also populations of the subspecies *pallidula, semifasciata,* and *annectens*). In summarizing, these authors wrote, "Of the 154 habitat categories . . . the 20 found most frequently are: everywhere (all sorts of situations) 18; woods 16; near water 13; lakes 12; fields 10; meadows 8; swamps 8; borders of rivers 8; marshes 7; along streams 6; gardens 6; roadsides 6; parks 6; clearings 4; margins of ditches 4; margins of creeks 4; moist situations 4; in water swimming 4; in water (otherwise) 4; low ground 4."

Thamnophis sirtalis shares most of its geographic range except the extreme northern part with other garter snakes; sometimes two or more kinds occur in one locality. The many forms involved must offer varying degrees of competition to *T. sirtalis* and must exert different selective pressures on its several geographic populations. In almost every instance where *T. sirtalis* occurs together with another kind of garter snake, *sirtalis* occupies the more general ecological niche, that which is most typical of the garter snakes as a group, whereas its competitor is more of a specialist. Throughout most of the eastern United States the ribbon snakes (*T. sauritus*

and *T. proximus*) are sympatric with *sirtalis* but careful comparison of habitat and food (Carpenter, 1952:238) has shown that the ribbon snakes are more aquatic, much more inclined to climb, confined to situations where there are thickets of shrubs, and more limited to amphibians as a food source. South of the Great Lakes *sirtalis* shares extensive areas with Butler's garter snake (*Thamnophis butleri*) and the short-headed garter snake (*T. brachystoma*), both stubby-bodied, terrestrial snakes adapted for feeding on earthworms. Throughout most of the Great Plains region *T. radix* is sympatric with *sirtalis*, but seemingly is less dependent on water. In the Southwest *T. cyrtopsis* and *T. marcianus* both overlap the range of *sirtalis* but occur far beyond its limits, in desert regions. Both are more aquatic than *sirtalis* and their occupancy of the limited aquatic habitats may prevent *sirtalis* from extending its range in that direction. In the western states the many members of the *elegans* complex include specialists in both aquatic and terrestrial habits. In localities favorable for garter snakes as many

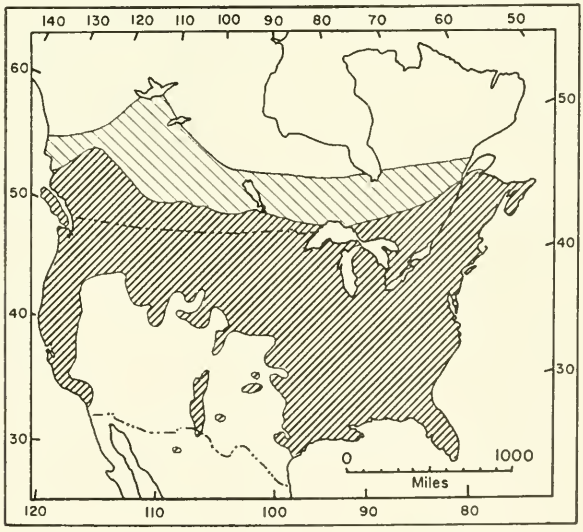


FIG. 3. Map showing range of *Thamnophis sirtalis;* the part in the United States and the southern edge of Canada (heavy lines) is shared with many other kinds of snakes, but a substantial part of the range (fine lines) lies to the north of ranges of all other snakes. Known range limits of *T. sirtalis* on the north correspond approximately with the northern limits of the Canadian Life-zone as mapped by Muesebeck and Krombein (1952:25). Distributional data are chiefly from Wright and Wright (1957) and Logier and Toner (1961).

as three members of this complex may occur along with *sirtalis* and their combined competition must be severe. At any rate, *sirtalis* is relatively stable and conservative in its habits and habitats as compared with the members of these groups.

Compared with its many partly sympatric competitors of other groups *T. sirtalis* has several traits that seem to confer distinct advantage and may, in part, account for its more extensive geographic range and (often) greater abundance locally. These are: 1. seemingly greater tolerance of low temperature sometimes resulting in a longer growing season, 2. larger average and maximum size, 3. larger litters of young.

TEMPERATURE RELATIONSHIPS

The range of *Thamnophis sirtalis* extends north far beyond the limits of any other reptile in the Western Hemisphere (Fig. 3). hence it perhaps has some special attributes permitting it to resist low temperatures. In the northern and central United States, where many other reptiles occur along with *Thamnophis sirtalis,* the latter is notable for early emergence from hibernation in spring, and persistent activity into late autumn. Bailey (1949:238) studied minimum temperature tolerances in garter snakes *(Thamnophis radix radix* and *T. sirtalis parietalis*) in artificial hibernacula at various depths, equipped with thermocouples. At depths down to 16 inches and at temperatures lower than —8° C. no snakes survived, but some did survive temperature as low as —2.2° and survived temperature of —1.5° or below for as long as two weeks consecutively. A temperature of —2.2° seemed to be near the critical level for *T. radix.* Whether the same applied to *T. sirtalis* was not definitely determined because only two individuals were used and both survived a temperature of —2.2°. Bailey concluded that garter snakes could regularly hibernate *above* the frost line surviving a temperature of approximately —2° C. because of gradual physiological preconditioning, the low temperature of crystallization of protoplasm, and possibly a limited capacity for "undercooling" of the tissues comparable to that found in invertebrates.

In February and March, 1964, I experimented with cold-tolerance in a group of *T. s. parietalis* from the Rockefeller Experimental Tract. The snakes were kept in a poorly heated room and usually their bodily temperatures were below 10° C. From time to time they were moved outdoors when the temperature of the air was near freezing or lower. Usually a Schultheis quick-reading ther-

mometer was taped in place in the snake's cloaca and other thermometers were kept nearby to check environmental temperatures. On many occasions snakes survived bodily temperatures between —2° and —3° C. and seemingly the critical minimum was near the latter level. On several occasions snakes that survived temperatures below —1° C. had their bodies much stiffened by partial congealing of their body fluids, but those that were frozen and completely rigid never survived. While cooling, the snakes moved about restlessly, trying to find shelter, and were capable of motion until bodily temperatures were at least one degree below freezing. However, they were soon immobilized and then gave the appearance of being anesthetized until they were warmed to several degrees above freezing. Although a bodily temperature of 3° C. or a little lower was lethal, the snakes were found to be able temporarily to withstand air temperatures that were considerably lower. On one occasion a snake was exposed at an air temperature of —9° for more than half an hour with no apparent harm, but the substrate was somewhat warmer and the snake's body was not completely frozen. Snakes that were too cold to move freely, and hence could not readily escape, were especially inclined to show fight, and would flatten their heads and bodies, coil, and strike with grotesquely slow motions. The lethal minimum for *Thamnophis sirtalis* is seemingly little, if at all, below those of other cold hardy snakes and does not suffice to explain the northward extent of the geographic range far beyond the limits of other species.

Carpenter (1953:78) found garter snakes (*T. s. sirtalis*) hibernating in crayfish burrows and vole burrows, both solitarily and in groups, sometimes partly or wholly submerged in water.

On the Reservation I found *T. sirtalis* to have a longer season of activity than any other kind of snake. Latest dates of record each year from 1949 through 1963 were in November, the 11th, 14th, 13th, 12th, 13th, 13th, 11th, 14th, 26th, 19th, 11th, 27th, 10th, 12th and 5th. All these late season records were of snakes caught in traps. An occasional individual may have been active on an even later date in some years, but certainly the bulk of the population retired somewhat earlier than indicated by the dates listed (see Fig. 4). In most years weather in late October and early November was often too cold for the snakes to be active, and their activity was therefore intermittent toward the end of the growing season, with an increasing proportion remaining in dormancy after the advent of each cold front. Earliest captures in spring were of snakes found

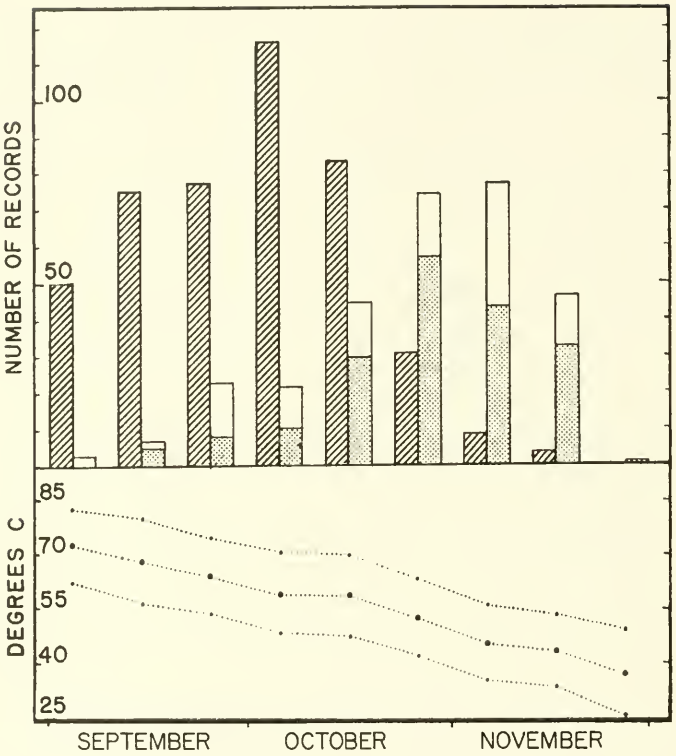


FIG. 4. Diagram showing numbers of garter snakes recorded at Reservation in autumn, in fields (left-hand, darker column of each pair) and along wooded hilltop with limestone outcrops (right-hand, lighter columns). Records are grouped in ten-day intervals, beginning with September 1 to 10 and ending with November 20 to 29. Left-hand columns represent combined data for years 1958 through 1963. Upper (unshaded) portions of right-hand columns represent these same years, and lower (shaded) parts of right-hand columns represent the years 1949 through 1957—when the trap lines were maintained only along the hilltop outcrops. Lower part of figure shows averages for the maxima, means and minima of daily temperatures (1949 through 1962).

in the open or beneath flat rocks, and trap lines were not set until well after the emergence of the snakes. Therefore in most years there was probably a considerable lag between the time garter snakes first became active and the time they were first recorded. On the other hand those snakes found in late February were certainly forerunners whose emergence preceded that of the main population because their hibernacula were in sites where premature warming occurred. It is my impression that in most years there are almost always one or more days in late March when some garter

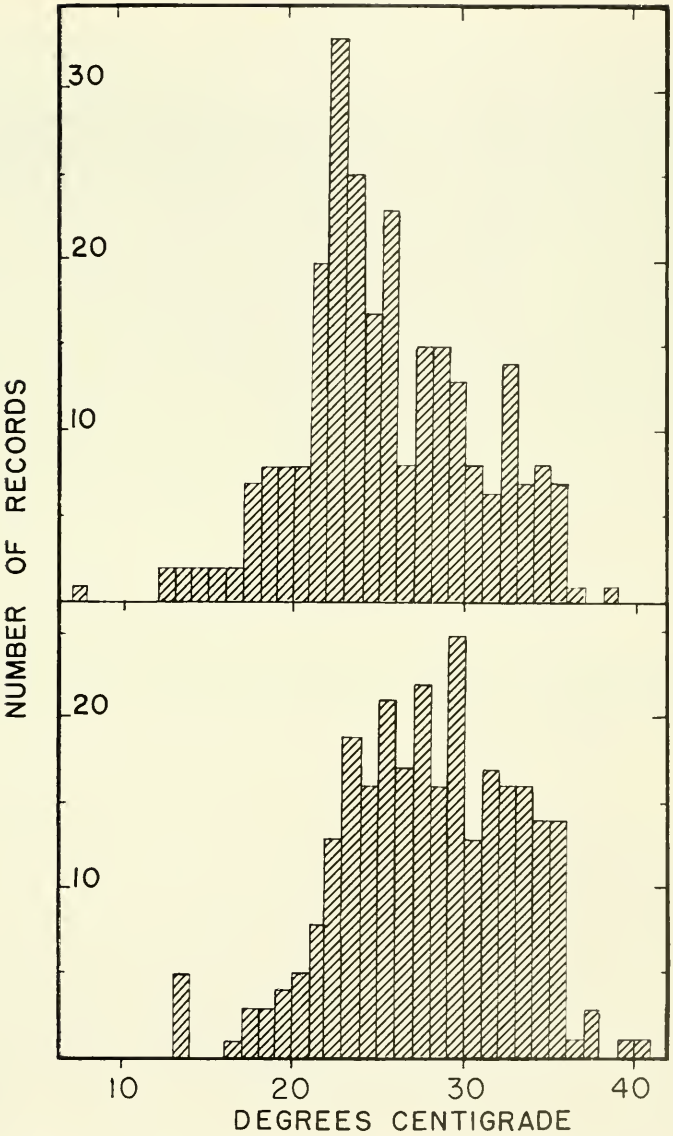


FIG. 5. Bodily temperatures (lower) of garter snakes found in live-traps at Harvey County Park; although confined, these snakes had some opportunity to regulate their temperatures, and seemed to prefer a level between 29° and 30°. Upper part of figure shows adjacent air temperatures, which averaged somewhat lower than the snakes' temperatures.

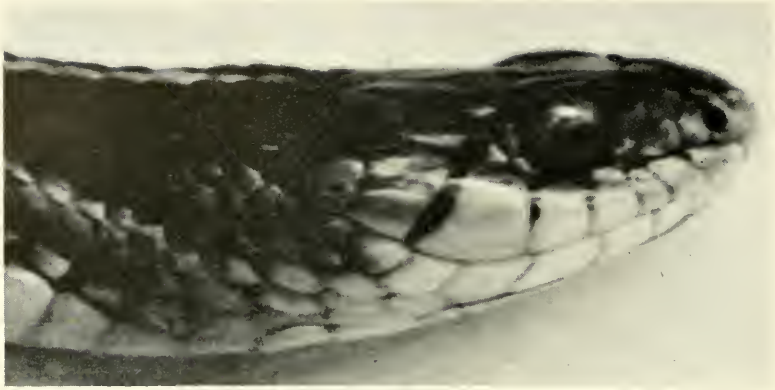


FIG. 1. Head of large adult female garter snake, *Thamnophis sirtalis parietalis* from lateral view, 2½ times natural size, The University of Kansas Natural History Reservation, May 18, 1964.

FIG. 2. Ventral aspects of adult garter snakes at posterior ends of bodies with tails to the left, showing typical differences in size and shape between the sexes; in the male (above) the tail, lodging the hemipenes, is slightly wider than the body, but in the female the tail-base tapers abruptly from the diameter of the body; May 19, 1964.

FIG. 1. Woodland pond near headquarters at The University of Kansas Natural History Reservation, Douglas County, Kansas, May 16, 1964, a breeding site for several species of frogs that provided the chief food source of garter snakes on the area. The snakes were often found about the margins of the pond, but also were well scattered over other habitats.

FIG. 2. Small pond in tall-grass prairie on the Rockefeller Experimental Tract, Jefferson County, Kansas, May 17, 1964; like the pond on the Reservation, this one was productive of amphibian prey, and garter snakes were abundant throughout the surrounding prairie.

PLATE 25

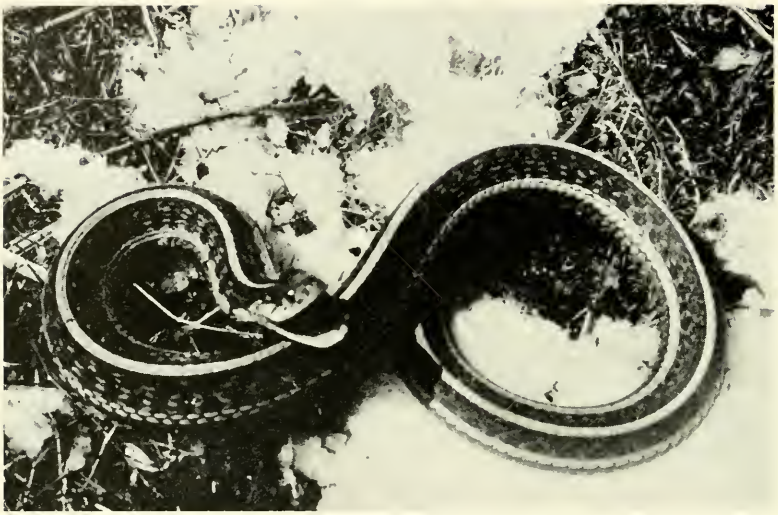


Fig. 1. Adult female garter snake in threatening defensive pose ready to strike, resting on patches of snow, illustrating the cold-hardiness of this species. Temperature of air was approximately 3° C. and that of the snake approximately 6° C. when this photograph was taken in March, 1964.

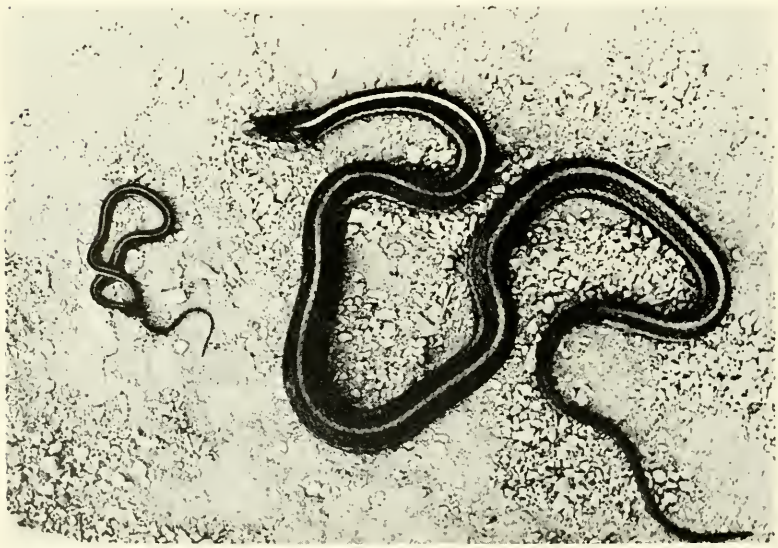


Fig. 2. Large adult female garter snake 773 millimeters snout-vent, 180 grams, and first-year young of typical size, 220 millimeters snout-vent, 4.0 grams on April 18, 1964.

snakes are active on the Reservation, and that there is intermittent but varying activity through early April. However, actual dates of first capture, 1950 through 1963, were as follows: April 10, February 28, May 7, March 25, February 24, April 3, March 26, April 10, April 15, April 4, April 12, April 18, May 12, May 8. For specimens from northeastern Kansas in the University of Kansas Museum of Natural History, the following dates represent the earliest records in several different years: March 28, 1910; March (exact date not given), 1912; March 2, 1927; April 1, 1930; April 9, 1933; April 12, 1934; April 9, 1939; April 11, 1941; March 31, 1947; April 6, 1949; April 12, 1950.

In several winters garter snakes were kept near the Reservation headquarters in outdoor cages having artificial hibernacula at depths of 15 to 36 inches. Several other kinds of snakes kept overwinter in the same enclosure suffered heavy mortality, but the garter snakes were remarkably hardy and nearly always survived. On February 11, 1961, when air temperature was 15.3° C., on the warmest day of the winter, two hibernacula were exposed to determine the condition of the snakes in them. The frost line was 13 inches below the soil surface. In a hibernaculum box at 30-inch depth temperature was approximately 4°, and snakes that were uncovered writhed feebly when touched. In a 15-inch hibernaculum temperature was 1.7°. A group of snakes were lying intertwined in a mass, but with their heads raised, seemingly aware of their surrounding and not fully torpid. All were in good condition.

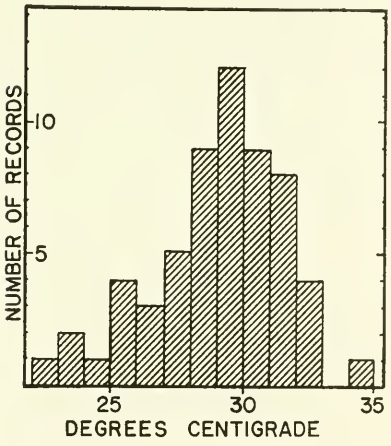


FIG. 6. Bodily temperatures of garter snakes confined in a cool cage, but with an electric lamp providing opportunity to bask. Definite preference for temperatures between 29° and 30° is indicated.

On May 20, 1960, tests of the relative cold-tolerance of several species of snakes were made. Two racers (young and adult), two adult ring-necked snakes, a small adult copperhead and a small adult garter snake were placed together in a plastic bag in a refrigerator. After 45 minutes they were removed. All were stiff and virtually immobilized (body temperature of one, 4° C.) but the

garter snake was the least affected. After a few seconds it began to crawl forward slowly. The ring-necked snakes soon became more active than the garter snake and one tested was found to have raised its body temperature to 12° C. Relatively rapid recovery in the ring-necked snakes resulted from their small size and high surface-to-mass ratio permitting relatively rapid absorption of heat.

The whole group was returned to the refrigerator in a slightly different spot. When they were removed after an hour body temperatures were 2° C. Again the garter snake seemed least affected in the first few minutes, but the ring-necked snakes, warming more rapidly at room temperature soon became more active and were able to crawl first. The group was returned to an even colder spot in the refrigerator and kept there for three and one-half hours. When removed all the snakes were partly frozen and appeared lifeless. Each of the two tested had a body temperature of —1° C. After 20 minutes the snakes were still partly frozen and were unresponsive to stimulation. After 50 minutes the garter snake and racers made slight response to stimulation, with slow, writhing movements. On the following day the garter snake and the smaller racer seemed to have recovered completely, but the larger racer was partly paralyzed, and the ring-necked snakes and copperhead were dead.

In June 1960 experiments were performed to test the heat-tolerance of several kinds of snakes. A garter snake was placed in a transparent plastic tube stoppered with cotton at each end, and with a Schultheis quick-reading thermometer inserted in the snake's rectum and taped in place. The snake's temperature was raised by exposing it to sunshine. As bodily temperature approached 40° C., the snake showed signs of discomfort and struggled violently to escape. At approximately 41° C. it collapsed and appeared to be dying, but was quickly revived by holding it in cold running water. A copperhead and ring-necked snakes subjected to the same treatment collapsed at approximately the same temperature, but a racer proved to be more resistant.

Lueth (1941:130) experimented with the survival of snakes at temperatures near their limits of tolerance. Two *Thamnophis sirtalis* survived for 48 hours at 41° C., but another died after 24 hours at 38.5°. On the Harvey County study area one garter snake when removed from a trap seemingly had died from overheating only a few minutes before and its rectal temperature was 40.5° C.

Opportunities to record temperatures of active garter snakes under natural conditions were rare. At Harvey County Park bodily

temperatures of many of the snakes found in traps were recorded, but these temperatures in confined snakes are of doubtful significance. Certainly these snakes had some opportunity to regulate their body temperatures by utilization or avoidance of occasional patches of sunlight, and contact or avoidance of soil, metal, and plant debris. But such opportunity for thermoregulation was limited and temperatures of the snakes tended to approximate ambient temperatures. Fig. 5 shows the distribution of these snakes' temperatures. They extended over a wide range, from 13° C. to 39° C. but with the greatest concentration between 29° and 30°.

On December 24, 1963, attempt was made to determine experimentally the preferred temperature level in a group of 21 adult *Thamnophis sirtalis parietalis*. The snakes were in a rectangular cage 36 inches long, 22 inches wide, and 28 inches deep, open on top and with a three-inch mat of straw on the bottom. The cage was in a poorly heated laboratory. A desk lamp was set in one corner of the cage, and turned on, with the bulb close to the bottom of the cage. Soon snakes attracted by the warmth emerged from the straw and approached the lamp to bask. A thermometer in the corner of the cage opposite from the lamp indicated a temperature there of 16.0° C. at the start of the experiment, and probably it deviated only slightly from this level during the several hours that observations were made. From time to time snakes basking in the warmth of the lamp were momentarily removed from the cage and their bodily temperatures were recorded. The histogram of Fig. 6 shows the trend of the 60 readings taken. As in the records of snakes removed from traps in summer, readings are most concentrated in the one-degree range, 29° to 30°, suggesting that these temperatures are most preferred. In this series the records are much more concentrated than they were in the trapped garter snakes; more than 81 per cent are in the six-degree range, 27° to 33°. Admittedly temperature preference in this species and in other ectotherms may vary according to physiological conditions, season, sex or age, and, perhaps geographic origin, and the limited data presented here provide only a crude approximation of the temperature preferences in *Thamnophis sirtalis*.

FOOD HABITS

In the course of my study exactly 200 records of prey items were obtained, of which 188 were palped from stomachs, and 12 were identified from scats. Seventy of these records originated from the Reservation; the remaining 130 were from Harvey County Park.

These records were as follows: 120 leopard frogs (*Rana pipiens*), 7 bullfrogs (*Rana catesbeiana*, all juveniles), 25 unidentified frogs (probably all either *Rana pipiens* or *R. catesbeiana*, but too far digested to be readily distinguishable), 12 American toads (*Bufo americanus*—all juveniles), 8 gray tree frogs (*Hyla versicolor*), 6 cricket frogs (*Acris crepitans*), 5 earthworms (*Allolobophora caliginosa*), 5 wood mice (*Peromyscus leucopus*), 5 western narrow-mouthed toads (*Gastrophryne olivacea*), 2 prairie voles (*Microtus ochrogaster*), and 1 each of harvest mouse (*Reithrodontomys megalotis*), garden toad (*Bufo woodhousei*), striped chorus frog (*Pseudacris triseriata*), bird (unidentified) and juvenal copperhead (*Agkistrodon contortrix*).

The trends of feeding differed somewhat on the two study areas, as might have been expected from the difference in habitat. At Harvey County 118 of the 130 items were ranid frogs, and predominantly leopard frogs (only two definitely identified as bullfrogs); the remaining items were 4 cricket frogs, 2 toads and a bird. Thus at Harvey County Park 91 percent of the food items were ranid frogs (chiefly *R. pipiens*); at the Reservation these same frogs made up the most important component of the food, but amounted to only 41.4 percent of the total, with a greater variety of miscellaneous items than were found at Harvey County. Besides the salientian amphibians, prey items consisted of voles, mice, a snake and a bird,

TABLE 3.—DISTRIBUTION OF 55 FOOD ITEMS OF GARTER SNAKES, ACCORDING TO SIZE OF SNAKE

	Snout-to-vent length of snakes in millimeters					
	200 to 299	300 to 399	400 to 499	500 to 599	600 to 699	700 to 799
mouse..... 4	...	...	.07	.06	.25	.17
frog (*Rana*).....28	.10	.12	.71	.59	.50	.66
tree-frog (*Hyla*)..... 8	.30	.12	...	.18	.25	...
Miscellaneous small salientian*.....14	.20	.62	.21	.18	...	.17
earthworm..... 5	.40	.12	...	...	...	...

* *Acris, Gastrophryne, Pseudacris* and newly metamorphosed *Bufo*.

eaten chiefly by large adult females, and earthworms, all eaten by juveniles.

The gray tree frog, the American toad and the copperhead, all recorded from the Reservation are not present in Harvey County. The Reservation is primarily upland habitat, and open water makes up much less than one percent of its area, but the Harvey County area is lowland of the Little Arkansas River Valley, with extensive marshy patches and numerous shallow ponds. Several kinds of frogs and toads breed in great abundance, but few are as numerous as the leopard frog. Populations of the leopard frog scatter into all habitats; they are neither secretive and subterranean like the spadefoot toad, chorus frog and narrow-mouthed toad, nor partly aquatic like the bullfrog and cricket frog. They are hence more available than any other species.

Earlier literature concerning the food habits of the red-sided garter snake consists of a few scattered records. These have been summarized by Wright and Wright (1957:858) who stated the food to be: "Insects, frogs, toads, small mammals, earthworms, spiders." Most published statements of the food habits of this and other garter snakes include insects. Remains of insects have often been found in the snakes' digestive tracts but in most instances they represent secondary items eaten by small vertebrate predators that were later ingested by the snakes. The chitinous exoskeletons of insects and other arthropods are remarkably resistant to the digestive juices of the snakes. Frogs and toads, especially, may gulp down relatively large insects intact, and themselves having no indigestible hard parts, may be subsequently eaten by a garter snake and leave no trace other than their insect prey. The 188 items palped from garter snakes included no insects, and captive garter snakes demonstrated no interest in insects that were offered for food.

The 219 scats that were collected and subjected to thorough examination under a dissecting microscope yielded only 12 vertebrate food items. In 130 of these scats there was nothing identifiable; the dried fecal mass consisted of black crumbly fine-grained almost homogeneous material, sometimes containing quantities of soil. The latter might have been interpreted as indicating predation on earthworms. Of the remaining 89 scats, only 8 had vertebrate remains exclusively; all others had remains of insects. In most instances the insect remains were fragmentary and were of medium-sized or small kinds, in contrast to the large and readily identifiable grasshoppers, crickets and katydids which made up the most im-

portant components of scats in racers, glass "snakes" and other insectivorous reptiles of the Reservation. In 59 instances the insects were identified as beetles, mostly small kinds, but including one occurrence of the large predatory carabid, *Pasimachus.* Often there were two or more kinds of insects represented in the same scat; in six instances minute beetles and ants were associated. It is almost inconceivable that either was a primary prey item of *Thamnophis;* probably the narrow-mouthed toad was the original predator in all these instances. With the possible exception of the *Pasimachus,* every occurrence of insects in the scats could be most satisfactorily explained as secondary prey originally eaten by a frog or toad.

Thamnophis sirtalis occurs in diverse habitats, over the greater part of North America and there is probably some geographic variation in its food habits beyond that enforced by availability. For instance, there is convincing evidence that *T. s. sirtalis* of the eastern states feeds on various insects, while such evidence is lacking for the western forms. For *T. s. sirtalis* earthworms seem to be a far more important component of the food than they are for the other subspecies. Nevertheless, throughout the widespread area of its occurrence the species seems to be remarkably stable in its habits.

Storer (1839:223) wrote that in Massachusetts *T. s. sirtalis* feeds upon frogs and toads. In Viriginia, Uhler, Cottam and Clarke (1939) found that in 24 stomachs earthworms made up 37 per cent of the food, salamanders 31 per cent, and toads 25 per cent. Conant (1951:107) reported that in Ohio: "A large portion of its diet is composed of frogs, toads, fish, earthworms and possibly insects." The same author questioned whether any of the insects were primary prey items and presented evidence to the contrary. The most extensive study yet made of food habits in the common garter snake is that of Hamilton (1951) in central and western New York. He examined digestive tracts of 382 garter snakes and found recognizable food items in 241. He found that earthworms (mostly *Lumbricus terrestris,* with a few *L. rubellus*) made up 63.5 per cent by volume and 56.9 per cent by frequency of the items taken. Amphibians made up 30.3 per cent by volume and 28.4 per cent by frequency. They included 31 frogs (*Rana sylvatica, R. palustris, R. clamitans,* and *R. catesbeiana*), 9 toads (*Bufo americanus*), 6 spring peepers (*Hyla crucifer*), and 17 salamanders (*Desmognathus fuscus, Plethodon cinereus, Eurycea bislineata, Ambystoma maculatum*). Other classes of items each made up less than five per cent, either by volume or by frequency. Slugs and snails (*Arion, Deroceras, Triodopsis, Anguispira*) were found only in juveniles. Insects also were found chiefly in immature garter snakes, and included various larvae (large sphingid moth, 3 tipulid larvae, more than 40 maggots), weevils, small carabid beetles, and in September several grasshoppers and crickets. The author made a convincing case that all these insects were primary items. Mammals (*Microtus pennsylvanicus, Tamias striatus, Blarina brevicauda*) were found in seven, and nestling birds (*Melospiza melodia*) in one. Fish (gold-

fish, horned dace, black-nosed dace) occurred in several. Crayfish occurred in four, sow bugs *(Oniscus)* in one juvenile, and snakes *(Storeria dekayi, Thamnophis sirtalis)* in three.

In Michigan Carpenter (1952:239) recorded 178 food items as follows: earthworms 80 per cent, amphibians 15 per cent, and the remaining small percentage almost evenly divided between mammals, fish, leeches, caterpillars and unidentified items. The high percentage of earthworms in this sample is perhaps due in part to the fact that Carpenter's records were compiled on the basis of frequency; on a volumetric basis they might have comprised a considerably smaller percentage. Carpenter's records indicated that the smaller snakes took a higher percentage of earthworms, and preyed mostly on smaller kinds of amphibians (*Pseudacris triseriata, Acris crepitans, Hyla crucifer*), whereas the larger snakes took mainly larger frogs (*Rana clamitans* and *R. pipiens*) and occasional mammals. Another important study in Michigan was that of Lagler and Salyer (1945). From 35 garter snakes taken in the vicinity of natural waters they obtained 111 food items including 50 earthworms, 33 toads (*Bufo americanus*—only two adults all others recently metamorphosed), 12 frogs (*Rana pipiens, R. palustris, R. sylvatica*), 6 fishes (*Salvelinus fontinalis, Notropis heterolepis*), 7 insects (beetles, grasshopper, moth) and one each of salamander, snail and leech. By way of contrast the same authors obtained food from 100 garter snakes collected about fish rearing stations. These contained a total of 273 items of which 115 were trout (*Salvelinus fontinalis, Salmo gairdnerii*). Also there were 8 occurrences of other fishes (*Umbra limi, Schilbeodes mollis*), 51 frogs and toads (mostly *Rana,* including one egg mass, and *Bufo americanus*), 50 earthworms, 39 insects, 4 mammals (*Microtus pennsylvanicus* and soricids), and 2 each of snails, salamanders and birds. Carr (1940:93) wrote that in Florida the leopard frog seems to be the staple food item, and that this garter snake also eats toads regularly.

Although occupying an even larger area than *T. s. sirtalis, T. s. parietalis* has been less thoroughly studied. In 48 stomachs of the Pacific Coast subspecies (*fitchi, infernalis, pickeringi, tetrataenia*) I found 72 food items; toads *(Bufo, Scaphiopus)* made up 30 per cent of the items, tree frogs (*Hyla regilla*) 21 per cent, earthworms 24 per cent, tadpoles 10 per cent, leeches 4 per cent, fish 3 per cent, and slugs 1 per cent (Fitch, 1941:31). Hebard (1951:62) wrote that in western Washington *Thamnophis sirtalis pickeringi* "feeds almost entirely on aquatic animals, particularly frogs and salamanders. The remains of a young bird were removed from one specimen." Batts (1961:350) found *T. s. pickeringi* foraging in tide pools and feeding on marine fishes including *Anoplarchus purpurescens, Xiphigaster atropurpureus,* and *Gobiesox meandricus.*

Because the young of *T. sirtalis* are remarkably small at birth in relation to the adults, many of the staple food sources available to the adults are unavailable to them. Even the smallest rodents and shrews of kinds eaten by adults are already too large at birth to be eaten by the newborn garter snakes. The same applies to the com-

mon frogs (*Rana catesbeiana, R. clamitans, R. palustris, R. pipiens, R. sylvatica*). The newly metamorphosed young of *Acris, Bufo, Gastrophryne* and *Pseudacris* are small enough to be eaten by the newborn snakes, but in northeastern Kansas, at least, parturition of the garter snakes is poorly timed to allow the young to utilize these potential food sources. Metamorphosis of the frogs and toads occurs chiefly in early summer, and by late July when the garter snakes are born the amphibians have mostly grown beyond the sizes that can be swallowed, and furthermore have dispersed and have undergone drastic reductions in numbers. Earthworms hence are probably the chief food source of the young, in most parts of the range, and their absence or unavailability in late summer may constitute a critical environmental factor, preventing the successful establishment of populations of this snake in areas where it might otherwise occur. This factor may explain the absence of *Thamnophis sirtalis* from large areas of the southwestern United States that have arid climates but nevertheless provide favorable habitat for various other species of garter snakes. In itself the competition of other species of the genus does not generally seem to be an effective factor limiting the occurrence or abundance of *Thamnophis sirtalis.* In the United States the latter is broadly sympatric with nine of the other eleven species of garter snakes. It is more generalized in habits, habitat and food requirements than are any of these other species; for instance it is less strictly terrestrial than *T. ordinoides, butleri, brachystoma* and *radix,* but is less aquatic than *T. proximus, T. marcianus, T. cyrtopsis,* or *T. elegans hydrophila.*

BREEDING

Blanchard and Blanchard (1942) have described in detail the mating of *Thamnophis sirtalis sirtalis* in southeastern Michigan. Their observations were made upon snakes confined in outdoor pits and kept for genetical experiments. The mating season at that latitude (42 degrees north) was found to extend from late March to early May, but was most concentrated in the latter half of April. Mating occurred when air temperature was above 60°F and the sun was shining. After several suitable days had passed, the snakes' sexual impulses seemed to wane, and courtship if it occurred at all was unlikely to be consummated.

The female was seemingly recognized chiefly by scent. Some females seemed to be more attractive than others to the males. Upon finding a suitable female, the male became animated in his

movements, pressed his chin against the female's back and slowly worked his way forward until he was lying extended along her with his cloacal region adjacent to hers. Spasmodic rippling movements passed forward along the male's abdomen and his tail-base was pressed against and beneath that of the female. Two or more males might simultaneously court the same female, but with no evident rivalry. Displacement of one male by another, such as occasionally occurred, appeared not to be purposeful but resulted from the usual vigorous courting movements. The female's role was mainly passive, but copulation could be effected only when she raised her tail (or permitted it to be raised by the male) allowing her cloaca to gape open and thus making possible the insertion of the male's hemipenis. This might be accomplished after courtship as brief as one minute, but typically five to ten minutes were required and sometimes more than an hour. As soon as an attachment had been made, the male's vigorous movements ceased and he slipped off the female. She usually crawled slowly forward, and the male was dragged after her with contact maintained only at the vents. Copulation was typically of 15 to 20 minutes duration. After separation occurred the snakes showed no further interest in each other. The female immediately became intolerant of courtship by other males, whereas the male might soon mate with a second female, or even with several in succession if he had the opportunity to do so.

Mating was found to occur also in autumn, especially on days of suitable temperature following periods of cold weather. In both fall and spring unconsummated courtship occurred frequently. Lack of success often was due to: 1) insufficiently high temperature, or 2) stage of the season, too early in autumn or too late in spring. Under these conditions females were usually unreceptive and males were languid and intermittent in their courtship. Females that were unreceptive vibrated their tails when approached by males, and made vigorous attempts to escape. Some of those that mated showed similar behavior at an initial encounter with a male, but were less vigorous in their attempts to escape, and eventually became pacified.

Rahn (1940:114) expressed the opinion that no "oestrus" period occurs in the females of *T. sirtalis* or other snakes. He stated that mating is not necessarily associated with ovulation or near-ovulation, nor is the endocrine basis for a mating urge associated with follicular growth. Rahn's study of the sequence of mating, ovula-

tion and gestation by the technique of excising small sections of the uterus from anesthetized females for microscopic examination established the fact that in the common garter snake several weeks normally elapse between insemination and ovulation. Rahn found that large mature females, whose oviducts contained motile sperm, often were seemingly not fecund, but had small and undeveloped ovaries.

In the winter of 1960-1961 a dozen adult garter snakes of both sexes were kept in an artificial hibernation pit in an outdoor enclosure at the Reservation headquarters. The pit was 15 inches deep and was 10 inches in diameter. A five-inch tile provided an entrance way, but for most of the winter it was plugged with a mass of excelsior. From time to time during the winter the plug was removed and the condition of the snakes was checked with a flashlight, or a thermometer in the pit was removed for a reading. On March 10, 1961, a sunny day with maximum temperature 65° F., the snakes were removed from the pit. When first observed they were partly submerged in water at the bottom of the pit and were in semi-torpid condition, but after a few minutes of basking in the sunshine they became fully active. Each of four males then began vigorous courting of the first female he met. Within an hour that temperatures remained favorable several matings were consummated and the sexual behavior followed exactly that described by Blanchard and Blanchard (*op. cit.*). In the females that had recently mated, the cloacae remained somewhat distended and partly filled with a semi-solid gelatinous mass of semen which seemed to form a copulatory plug comparable to that in some rodents. Sexually aroused males could not be induced to court recently mated females, and seemed to have a definite preference for unmated individuals, but the sensory basis for such discrimination was not evident.

Sexual behavior was observed on only a few other occasions. In two different years when females had been kept over winter in outdoor enclosures, and had emerged in early spring, males not enclosed with them were found within a few feet providing circumstantial evidence that the scent of the female may attract a male from a distance, and that he need not necessarily follow her trail to find her.

Gardner (1955:310) also made significant observations indicating that females are located by airborne scent. On April 18, 1955, at Seymour, Connecticut, he observed a "snake ball" of garter snakes during its formation. At first there were four or five in the group,

but others gathered from various directions until there were 15 or 20. One relatively large snake, presumably a female, was the center of attraction, and when this individual shifted to a slightly different location, the rest of the group was thrown into confusion. Gardner later (1957:48) described a second "snake ball" at the same locality. When most of the snakes dispersed a copulating pair remained. Wright and Wright (1957:839) cite an instance of males trailing a female by scent, duplicating her route and finding her on a low branch of a tree. Wright and Wright cite instances of spring breeding aggregations. Fox (1955:176) reported mating aggregations of *T. s. tetrataenia* in late October and early November.

A mixed group of adults was kept through the winter of 1963-1964 in a laboratory building in which air temperature was usually between freezing and 16° C. On several occasions in December and January when a lighted desk lamp was set in the cage, snakes were warmed to activity and desultory courtship was observed, but it was not known whether copulation occurred.

The annual cycle of the male reproductive organs in *Thamnophis sirtalis* and *T. elegans* has been described by Fox (1954); that of *T. radix* has been described by Cieslak (1945). It is remarkable that despite a short breeding period, the male of *T. sirtalis* has active mature spermatozoa throughout most of the year. Sperm are matured in the latter half of summer. Cloacal smears were obtained from many of the male garter snakes checked in my field study. Three adults were checked in June 1959. In one of these no sperm could be found; the other two contained abundant dead sperm. Most adults caught in other months had living sperm. One of the smallest individuals having motile sperm was 389 millimeters in snout-vent length, and weighed 21.5 grams on July 24, 1960, when presumably he was a little less than one year old.

Cloacal smears also were taken from females and microscopically examined for living sperm as evidence of recent mating. One in April was positive, but several in summer were negative. In the autumn months the following percentages were positive: 6.25 per cent of 16 examined in September; 22.7 per cent of 22 examined in October; 50 per cent of eight examined in November.

Number of Young in Brood

In a total of 132 females checked by palping their abdomens or kept until they gave birth to litters, the total egg count was 2012, indicating an average brood of $14.5 \pm .031$. Brood size ranged from four to 29, but 91 per cent were within the range seven to 20 (Fig. 7). It is a common observation on garter snakes and other viviparous snakes that some of the eggs ovulated re-

main unfertilized, that embryos often develop abnormally and sometimes are aborted, and that even those surviving until the time of normal parturition are sometimes born dead. Therefore the average litter is probably smaller than the numbers obtained from counting eggs.

Six of the females that had been checked for numbers of eggs were recaptured one or more times in the course of their pregnancies. First captures were from May 14 to June 22 and later captures were from June 10 to July 17, with an average interval of 27 days. In each of these individuals the egg count obtained on the later date was smaller than the count obtained originally, by from one to six eggs, with the total number being reduced by 24 per cent, from 83 to 63. Although care was taken not to injure the snakes in handling and palping them, there is some chance that even the gentle pressure of the fingers on the eggs, and the slight momentary displacement of the eggs involved may have been harmful and resulted in losses. The losses during pregnancy were further tested by averaging the number of eggs found in females in each month of the period when the snakes are gravid. The numbers obtained from females not previously palped were as follows: May 15.2, June 14.3, July 13.8. These figures suggest a loss of about 4.6 per cent per month during pregnancy. In eleven seemingly normal litters born in captivity the number of young averaged 13.5 and ranged from five to 22. Perhaps the average clutch has between 15 and 16 eggs at the time of conception, and is reduced to between 13 and 14 eggs during pregnancy. Some further reduction may occur at the time of birth. The much higher loss indicated by the females palped and recaptured presumably must be attributed to the harmful effects of palping.

In many other species of reptiles it has been observed that primiparae produce relatively small complements of eggs or young, and that in successive seasons as the individual becomes older and gains in bulk, she produces progressively larger broods. This trend is demonstrable in *Thamnophis sirtalis*. The youngest females that produce young are approximately two years old at the time of parturition, but at the time of conception are little more than 21 months old. Most of the females involved were measured at some time between conception and parturition and doubtless would have made some further growth in length and bulk before the end of their pregnancies, which coincided rather closely with their own birth dates. On the basis of available data on growth as summarized in the following section, each individual female recorded was somewhat arbitrarily assigned a "most probable age," and correlation with size of brood was indicated, as shown in the following list.

27 two-year-olds (504 to 580 mm.) average 12.0 ± .142 ova
45 three-year-olds (585 to 660 mm.) average 13.0 ± .082 ova
39 four-year-olds (668 to 738 mm.) average 16.8 ± .134 ova
16 five-year-olds (740 to 786 mm.) average 16.5 ± 1.13 ova
6 six-year olds (795 to 815 mm.) average 16.3 ova

Four individuals that ranged from 844 to 950 mm in length and may have been more than six years old, had, in order of increasing length 9, 12, 17 and 18 ova with an average of only 14—less than the numbers found in four-, five-, or six-year olds. Blanchard and Blanchard (1942:232) mentioned a large old female that produced six litters in successive years of captivity, but then ceased to produce young seemingly having become sterile as a result of senility. Blair (1960:96-97) found that in the rusty lizard (*Sceloporus*

olivaceus) productivity increased greatly in females from the first to the second year and the second to the third, but that it was somewhat reduced again in the relatively small number of females that survived beyond the third year. For garter snakes and for reptiles in general, a consideration important in population ecology is whether females that survive beyond the average life-expectancy continue to produce successively larger litters, or whether after a few years litter size undergoes reduction—even to the vanishing point as post-reproductive status is attained.

In some kinds of snakes a certain proportion of the adult females in any one year do not produce eggs or young. A definite biennial cycle may be involved, notably in northern viperids and crotalids, or rarely the cycle may be even longer than two years. In the garter snakes and probably most other common snakes of the United States the cycle is normally annual, and the non-breeders are those that have failed to attain sexual maturity or have not been inseminated, or are inhibited from producing eggs by undernourishment or pathological conditions. Of 181 adult females palped for eggs in May, June and July, 58 (32 per cent) were definitely not gravid. In southeastern Michigan, Carpenter (1952:253) found 35 per cent of the females in a large sample to be non-gravid. Axtell in New York found between five and 20 per cent of the females to be non-breeders (in a series totalling 1414). He noted that many of the non-breeders were only slightly above the minimum size of pregnancy and hence probably had not yet attained sexual maturity (Wright and Wright, 1957:838). Hebard (1951:177) found 33 per cent of adult females to be non-gravid in a series of 66 *Thamnophis ordinoides* from western Washington. In my own study the incidence of non-breeders showed a definite correlation with age. Using the same arbitrary age-size correlation shown above for average size of broods, the following percentages were obtained:

Of 62 two-year-olds, 42 per cent were gravid
Of 57 three-year-olds, 58 per cent were gravid
Of 40 four-year-olds, 93.5 per cent were gravid
Of 12 five-year-olds, 83 per cent were gravid
Of 6 six-year-olds, 100 per cent were gravid
Of 4 seven years old or more, 100 per cent were gravid

Many previous writers have made general statements concerning the sizes of litters in *Thamnophis sirtalis* or have published specific figures of numbers of young born or embryos found in gravid females. However, the literature provides only two substantial samples. Carpenter (1952:253) recorded an average of 18 young born to 20 females of *T. s. sirtalis* from various localities in Michigan. Zehr (1962:324) found 1225 embryos in 104 gravid females of *T. s. pallidula* in New Hampshire—an average of 12.9.

Blanchard and Blanchard (1941:179, 181, 183, 185, 186; 1942:228) have published records of litters born in captivity to females collected in Michigan and kept for genetical studies. The sample had approximately the same geographic origin as Carpenter's, but the litters averaged larger, 23.2 (51 to 6) in a sample of 31. The figures probably are not strictly comparable with those of egg-counts or of litters born to females recently removed from natural conditions. The captive females were copiously fed and many of them were successfully kept for periods of years, producing successive annual litters and attaining a bulk and productivity greater than that of a typical individual in a natural population.

The records accumulated in the course of my study, supplemented by the figures published by Zehr and Carpenter, provide a large sample of 256 gravid females with a total of 3597 embryos, and these seemingly justify the conclusion that the litter size averages between 12.9 and 18 with some geographic variation.

Strangely enough, other published records do not bear out this conclusion, but indicate a much higher reproductive potential. Several authors have published figures purporting to represent the litter size of the garter snake, without presenting specific records, for example: 13 to 80, Seiss (1890:105); 10 to 70, Funkhouser (1945:14); 14 to 78, Smith (1956:293). A number of other authors have published specific records of litter size but, obviously of litters which were mentioned only because they were considered unusual: 85 in Michigan (Martof, 1954:100), 80 in Ohio (Morse, 1904:140), 78 in Illinois (Schenck, 1883:1008), 74 in Massachusetts (Wallace, 1938:203), 72 in Indiana (Reddick, 1896:261), 64 in Ohio (Mattlin, 1948:149), 53 in Illinois (Cagle, 1942:193). Although there is no reason to question the authenticity of any of these records, it is obvious that they are not typical of the species.

Eliminating these unusually large litters and certain published records that seem to be based on guesses or on vaguely remembered observations, I have accumulated from the literature records of 100 broods (or batches of developing embryos) from *Thamnophis sirtalis sirtalis* which seem to be authentic. Many of these records were summarized by Wright and Wright (1957:840-841) who have reviewed the literature rather thoroughly, and those

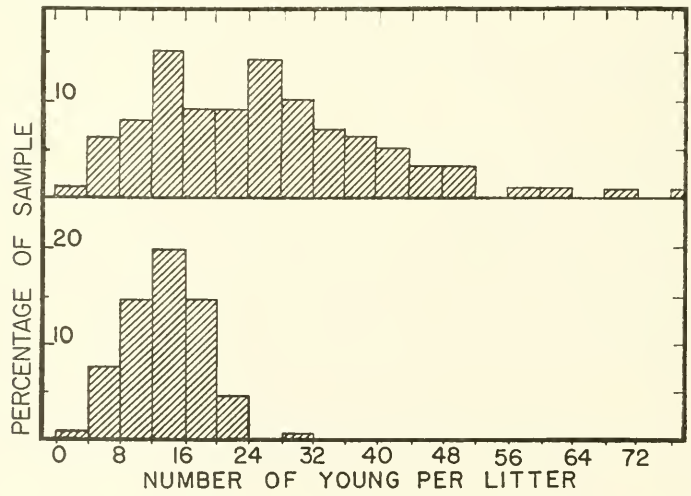


FIG. 7. Size of litter in *Thamnophis sirtalis* as indicated by eggs palped or dissected from gravid females, or numbers of young born in captivity. Upper histogram shows 100 records from published literature for *T. s. sirtalis;* lower histogram shows field records from the present study for *T. s. parietalis* at the Reservation and Harvey County Park. The different trends are believed to result chiefly from bias in the literature sample, arising from the fact that authors tend to be selective in obtaining and publishing records of the larger litters and geographic trends in size of litter are probably of minor importance.

in the following list that are marked with an asterisk have been accepted from their summary without my having seen the original publications. Average for the entire group was 26.

The records were as follows: 7, 11, 21, 42 (Axtell *), seven litters of from 10 to 21, averaging 15.5 (Barbour, 1950:105), 14 (Barton, 1952:190), 12 (Bishop and Alexander *), 27 (Boyer, 1941:334), 3, 20, 50, 61, 72 (Breckenridge, 1944:149), 37 (Breder and Breder, 1923:22), 13, 15, 16, 17, 18, 30, 32 (Burt *), 27 (Clark, 1949:257), 6, 8, 10, 12, 13, 14, 15, 16, 22, 23, 27, 30, 33, 39, 75 (Conant, 1943:169; 1951:107 and 252 and *in* Wright and Wright), 31 (Conant and Downs, 1940:46), 30 (Cook *), 8, 11, 11, 16, 28, 31, 51, 27, 30 (Ditmars, 1936:152 and *in* Wright and Wright), 14, 28, 40 (Fowler*), 13 (Garman*), 35, 39 (Hay, 1891:110), 18 (List, 1950:71), 12, 24, 26, 27, 31, 34, 49 (Logier, 1929:83; 1930:20), 8, 21, 24, 24, 25, 35, 41, 42, 44, 45, 48 (McCauley, 1945:127), 21 (Meade, 1934:5), 33 (Milnes, 1946:11), 38 (Patch, 1919:60), 30 (Pope *), 42 (Putnam, 1869:34), 31 (Ramsey *), 27 (Smith, 1961:233), 25, 40 (Smith *), 36 (Triplehorn, 1955:248), 35 (Welter and Carr, 1939:129), 20 (Williams, 1942:92), 57 (Wood, 1945:118), 17, 27, 39, 45 (Wright and Allen *), 19 (Wright and Simpson *), 8, 25 (Wright and Bishop, 1915:184).

Obviously garter snakes occasionally produce litters much larger than any found in my own study. Geographic differences may be involved, since all the largest litters recorded, those having more than 50 young, have originated from the Great Lakes Region and the northeastern states.

It is remarkable that the average for all these litters is nearly twice the average found in my own field study, and that nearly one-third of all these literature records exceeded in number the largest litter recorded by me. It might be suspected that geographic variation accounts for the difference, but this idea is not substantiated by an analysis of the records. Thirty-four records for the northeastern states (Massachusetts, New York, New Jersey, Pennsylvania and Maryland) averaged 25.5, and 49 records for the Great Lakes region (southern Ontario, Ohio, Indiana, Illinois, Michigan and western Minnesota) averaged 27.3. Eight from the southern states—Florida, Georgia and Louisiana —averaged only 24.4.

Carpenter's series from Michigan averaging 18 and Zehr's larger series from New Hampshire averaging 12.9 do not bear out the idea that litters in these regions average larger than elsewhere. It seems that in most instances large litters are produced by females that are exceptionally large and, presumably, old. In a local population the productivity would depend in part on the age structure. Food supply and other variable environmental factors also would have important effects. Abnormally large litters probably could be produced only under optimal environmental conditions.

For the western subspecies records of litters are relatively few. Twelve litters of *T. s. parietalis* (Over *; Gadow *; Gloyd, 1928:131; Anderson, 1942: 214; Munro *; Hudson and Davis, 1941:1; Carpenter, 1958:113; Hudson, 1942:79; Gehlbach and Collette, 1959:143) averaged 30. Eighteen litters of the West Coast subspecies *concinnus, fitchi* and *infernalis* (Ruthven, 1908; Fisher, 1928:221; Ditmars,* Bogert,* Wright and Wright, 1957:848, Hart,* Patch,* Rothman and Rothman, 1960:101; Tanner *) averaged 14.5 young and two broods of *annectens* (Curtis, 1949:10; Werler, 1951:45) averaged only nine young.

Since the garter snake is notorious for its high reproductive potential, authors probably have been somewhat selective in tending to publish the higher counts and to disregard the lower counts of embryos or young. Several records of

the largest litters have been published because they exceeded in number any previous records, or were thought to exceed them. Because of the species' abundance persons wishing to obtain litters of young are often able to secure fecund females in ample quantities, and would tend to retain the largest and most obviously gravid individuals, but perhaps would discard those that were smaller with less evident signs of pregnancy. In the resulting litters the average number of young would be considerably higher than in the average litter born under natural conditions.

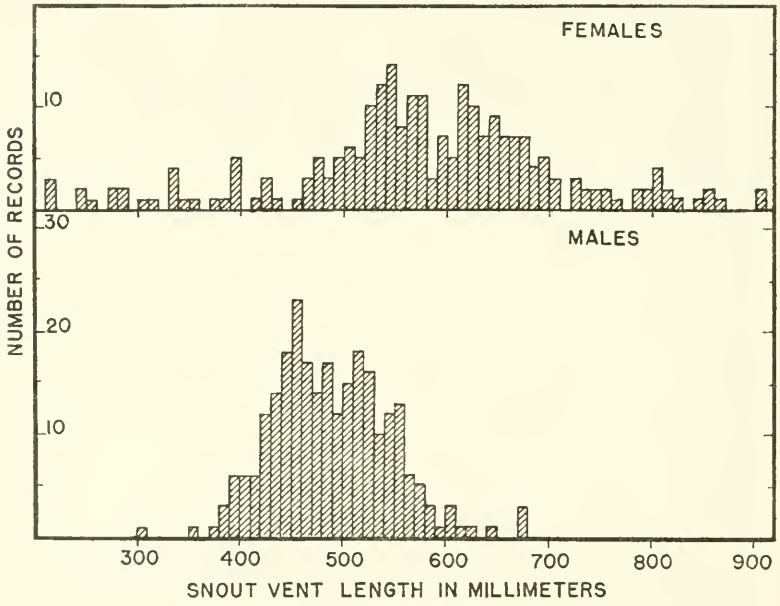


FIG. 8. Size distribution in an autumn sample (September 1 through November 30) of garter snakes from the Reservation, 1949 through 1963. Recently born snakes and one-year-olds are poorly represented because they are not retained by the traps. Third-year snakes comprise the most numerous group and are larger in females (average about 550 millimeters) than in males (average about 450 millimeters). Successively older age groups form indistinct peaks further to the right on each histogram.

Timing of Breeding Cycle

Records indicate that throughout the range mating normally occurs soon before hibernation (October and early November) or soon after emergence (chiefly April, but sometimes in March or early May). Blanchard and Blanchard (1942:176) found that in southern Michigan development (final maturation of ova, ovulation, and gestation) for the population as a whole required as much as 116 days in the cool summer of 1935 and as little as 87 days in the unusually hot summer of 1934. For the years of their study an increase of one degree in average temperature hastened the time of birth by about four and a half days. As in my own field study, late July or early August were found to be the usual time for birth. Conant (1951:107)

recorded births as early as July 3 in Ohio, and Meade recorded a litter born on June 24 in southern Louisiana. At the other extreme Rahn (1940:112) found that in the cool, damp habitat of Penikese Island off the coast of Massachusetts garter snakes were still dispersing from their winter quarters at the end of May and did not ovulate until June, or until early July in one instance. Milnes (1946:4) recorded a litter born at Oxford, Ontario, on October 9, 1933. Two published records deviate notably from the normal timing of the breeding cycle: Barton (1952:198) recorded a female of record size from Florida (received from Ross Allen's Reptile Institute) which produced a litter on May 31, 1952, and Triplehorn (1955:248) reported a female from Broward County, southern Florida, which produced a litter on January 11, 1952. Seemingly in the semitropical climate of southern Florida the breeding cycle that prevails throughout temperate North America may be much altered because a well-defined winter season of dormancy is lacking.

GROWTH

The garter snakes in any population consist of a number of discrete age groups, since the females give birth to their young within a relatively brief period in late summer. The newborn young are remarkably small as compared with their mothers. In 151 newborn garter snakes of litters born in captivity, snout-vent length averaged 167.9 ± .865 millimeters (191 to 134) and weight, 1.88 ± .029 grams (2.5 to .7).

For a newborn garter snake the chances of survival are poor, and juvenal garter snakes, even those beyond half-grown size, passed readily through the quarter-inch mesh of the wire used in construction of my snake traps. Therefore records of juveniles were relatively few, and their rare recaptures were inadequate to show their usual growth rate. An exceptional record pertains to a female caught and marked on August 5, 1959, when she had a snout-vent length of 170 millimeters and a weight of 2.7 grams—still within the size range of the newborn, and almost certainly less than two weeks old. She was recaptured on June 20, 1961, and in the 22½-month interval (of which approximately ten months, during two winters must have been spent in hibernation) had grown to adult size (608 millimeters, 161 grams) and was gravid, with 17 eggs. In the light of other evidence, it seems that this female was fairly typical in her growth.

Juveniles with snout-vent lengths of less than 200 millimeters are found chiefly during a period of a few weeks following parturition, in late summer and early autumn. Juveniles within the size range 200 to 300 millimeters are found mostly in autumn and spring, but not in summer when, presumably, they have passed beyond this stage of growth. The average size of juveniles at any one time provides an indication of their growth.

A serious obstacle to the calculation of growth by this method is that some grow so rapidly and some so slowly as not to be readily identified with their age group. August 1 is probably near the mean birth date, but some young are born in the last week of July and others in the second week of August or even the third. The known range in length of the newborn, 191 to 134 millimeters, is therefore much increased by the time the latest young are born, and is further increased by the time of hibernation. Even in one year there is some difference between individuals in time of retirement into hibernation, and the average date may vary as much as two weeks from one year

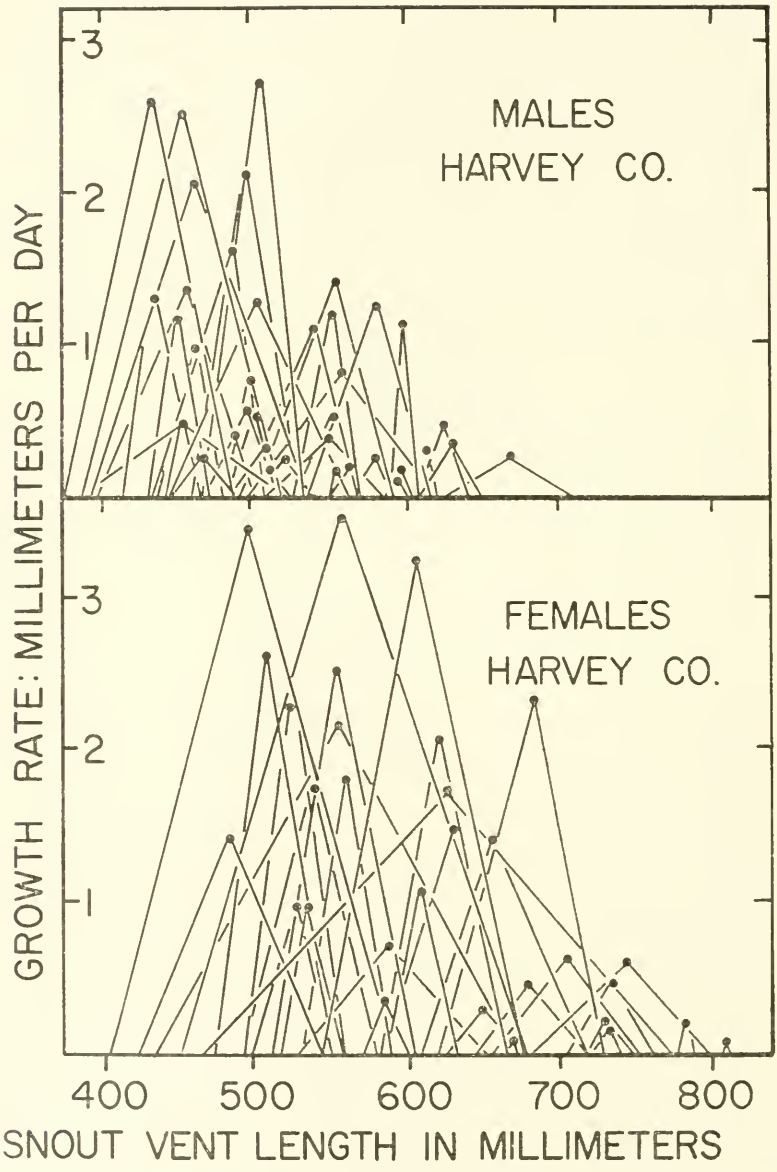


FIG. 9. Individual growth rates (gain in millimeters per day in snout-vent length) of garter snakes at Harvey County Park that were marked and recaptured. Growth rate is shown to be highly variable with marked differences between individuals but on the average females grow faster than males. In all instances snakes recaptured after an intervening winter were assumed to have made no growth during the months November through March, and in calculating the growth rate this period of probable dormacy was excluded.

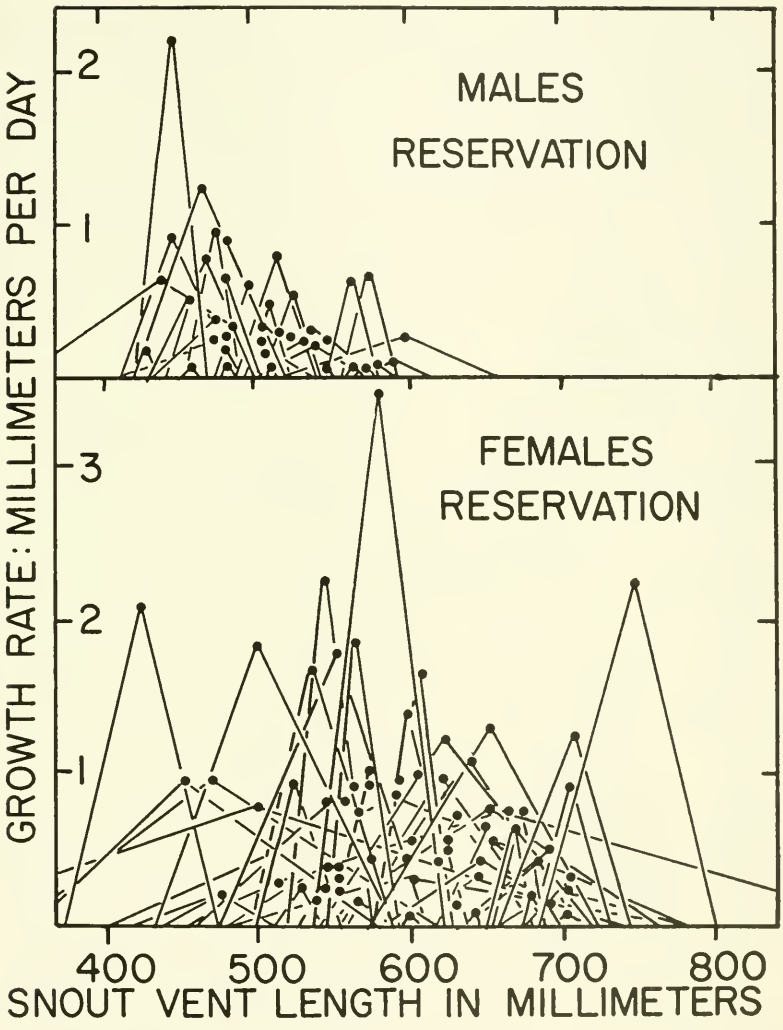


FIG. 10. Growth rates in garter snakes at The University of Kansas Natural History Reservation and Rockefeller Experimental Tract, shown as in Fig. 9. The trend of growth in this group of snakes is less rapid than in the group from Harvey County Park, probably because of a less abundant food supply.

to another. Therefore it is not surprising that the first-year snakes emerging from hibernation in spring cover a fairly wide size range.

In the University of Kansas Natural History Museum are 22 juvenal garter snakes from northeastern Kansas collected in late March or April (average date April 9) of nine different years. Snout-vent lengths of these young, all thought to be first-year individuals, were recorded as follows: 370, 340, 325,

312, 310, 310, 300, 300, 275, 275, 265, 265, 260, 260, 245, 242, 240, 235, 235, 235, 228. The entire group averaged 276 millimeters, hence had gained on the average, approximately 108 millimeters over the usual length at birth. At the time of preservation most of these young must have been a little more than eight months old, but from about mid-November until late March they must have been hibernating, and had had an estimated 84 days of active life, on the average. Their length increments represent an average gain of 1.3 millimeters per day of active life, but for different individuals the figure varies from as little as .7 millimeter per day to as much as 2.7 per day.

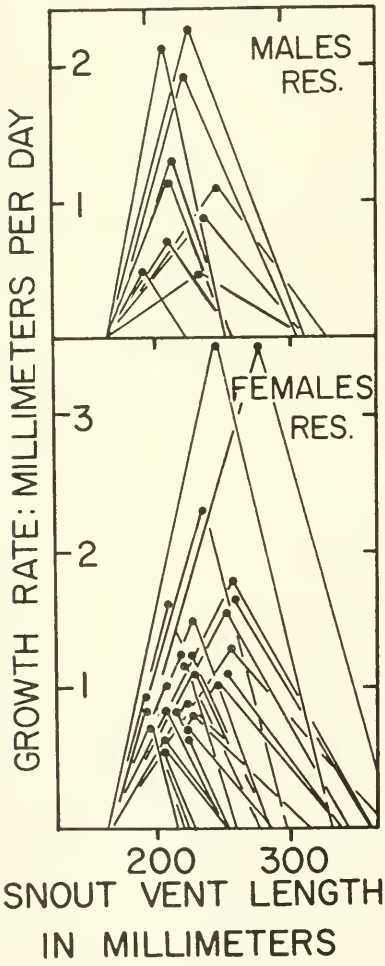


FIG. 11. Probable growth rates in young garter snakes captured on the Reservation and Rockefeller Tract; for each the rate was calculated on the assumption that the snake was of average size (about 168 millimeters snout-vent) at birth, was born on August 1, and hibernated from November 1 through March 31.

For 33 young caught on the Reservation in different years in September, October, November, April and May, the average length gain per day was calculated to be $1.10 \pm .062$ millimeters—on the assumption that they were born on August 1, and that those caught in spring had hibernated from November 1 through March 31. The average growth for ten males was 1.03 millimeters per day whereas that for 23 females was 1.14. More rapid growth is to be expected in the females since they attain a larger adult size.

On June 7, 1950, a juvenal male having a snout-vent length of 260 millimeters was recorded and this was one of the most retarded young captured. Assuming average size at birth, he had grown .57 millimeters per day in an estimated 160 days of growth. Other first-year young caught in June were all more than 300 millimeters in length, and some of them could not be readily distinguished from second-year individuals. The combined samples from the Reservation and from Harvey County contained 48 snakes caught in June that were judged to be first-year young, and for the entire group the average snout-vent length was 372 millimeters, indicating an average increment of 1.2 millimeters per day of active life. For the 25 males length averaged 365 millimeters and for 23 females it averaged 380, indicating daily length increments of 1.16 and

1.25 millimeters, respectively. Probably growth slows in the period of weeks preceding hibernation and the period immediately after emergence, as would be expected from the reduced rate of metabolism in cool weather of autumn and spring. At any rate the most rapid growth measured in recaptured individuals was recorded in summer. Up to early summer the first-year males and females seem to differ only slightly in size, but the samples have too few snakes to show accurately the difference in size between the sexes up to this age.

In older immature snakes, age-groups are somewhat obscured by overlapping in size. However, the course of growth can best be traced by examining the size distribution of samples from different times of year. Fig. 8 shows the size distribution of garter snakes caught on the Reservation in autumn—the months of September, October and November combined. This sample is far larger than those obtained in any comparable periods. It shows that in autumn adult males are most abundant in the length range 430 to 480 millimeters. It seems certain that these represent the same group of males which measured 365 millimeters in mid-June. In approximately 138 days of additional growth they had added on the average about 85 millimeters, an increment of .62 millimeters per day. Males become sexully mature at a snout-vent length near 400 millimeters, and seemingly sexual maturity slows their subsequent growth.

The length range of 430 to 480 millimeters, which contains the greatest number of males in autumn, contains relatively few females. Instead, the adult females are most concentrated in the length range 520 to 580 millimeters snout-vent length, and evidently these are 15-months-old individuals, of the same group that averaged 380 millimeters in mid-June. In the 138-day interval they have gained approximately 165 millimeters, an increment of about 1.2 millimeters per day. Throughout the summer and early autumn these females have thus gained at approximately double the rate of their male counterparts, and have maintained the same rapid growth rates characteristic of both sexes during their early months of active life.

Growth after attainment of subadult size (approximately 400 millimeters snout-vent length in males and 500 in females) is well shown by numerous individuals marked and later recaptured after substantial intervals. The most noteworthy fact concerning growth in *T. s. parietalis* is the great difference between individuals (Figs. 9, 10 and 11). Genetic differences are probably involved, but varying availability of food from time to time and place to place is probably the one most important factor determining the amount and rate of growth. At the Reservation the lowest growth rates were recorded in the

TABLE 4.—SIZES AND CALCULATED RATES OF GROWTH OF JUVENAL GARTER SNAKES ON THE RESERVATION

	Number of young in sample	Average size of young	Calculated growth rate per day since birth
August	14	209(297–158)	2.00
September	15	216(330–148)	.96
October	18	263(344–171)	1.27
April-May	20	296(350–215)	1.16
June	48	372(426–298)	1.20

drought years of 1952, 1953 and 1963, whereas much better growth was made by most individuals recaptured in 1959 through 1962, when precipitation was adequate to promote successful breeding of the common species of amphibians, and to make earthworms frequently available on the surface of the soil.

The summer of 1963 was the second driest on record in the region of my study. Young garter snakes were born mostly in the last week of July and the first week of August. Several females in confinement produced litters from July 26 to August 2, and after the latter date no gravid females were found. Young were found subsequently as follows: on September 15—183, 175, 170 and 164 millimeters (snout-vent); September 25—148 millimeters; September 26—188, 170 and 185 millimeters (the latter a recapture, the same individual that measured 183 millimeters on September 15); October 2—209, 206 and 171 millimeters; October 7—301 millimeters; October 15—213 millimeters; October 26—196 millimeters. Of these 13 young only the one caught on October 7 had made substantial growth. The others, even up to a probable age of three months, were still within, or near, the size-range of the newborn. Larger garter snakes also made minimal growth in 1963. Table 5 shows changes in lengths and weights of all those caught at least twice in 1963 with substantial intervening, or caught at the end of the 1962 growing season and again in 1963. Dates are all in 1963 except where otherwise indicated. Three of the snakes were recorded as slightly shorter on the later date of capture than on the earlier date. Actual shrinkage probably did not occur but in each instance the apparent loss was less than two per cent—within the expected range of error in measuring.

In the summer of 1959 rainfall was above normal. Only four young of the year were caught, but all had made growth better than average, as follows:

TABLE 5.—SLIGHT GROWTH OR LACK OF GROWTH IN 1963 IN INDIVIDUAL GARTER SNAKES MARKED AND RECAPTURED

Sex	Original Record			Recapture Record		
	Date	Snout-vent length in millimeters	Weight in grams	Date	Snout-vent length in millimeters	Weight in grams
♂	October 10*...	528	38	July 21.....	542	40
♀	May 27.....	540	60	September 15..	548	55
♀	June 26.....	576	92**	August 3.....	577	56
♀	May 30.....	545	65**	October 23....	560	52
♀	May 8.....	572	70	October 19....	630	79
♀	June 5.....	592	38	September 10..	612	70
♀	June 5.....	628	100	September 15..	625	90
♀	May 8.....	624	90	July 19.....	616	103
♀	September 18*	736	119	July 23.....	730	.....
♀	June 25.....	735	164	October 19....	735	132

* 1962
** gravid

TABLE 6.—GROWTH IN INDIVIDUAL GARTER SNAKES MARKED AND RECAPTURED IN 1959

Sex	Original Record			Recapture Record		
	Date	Snout-vent length in millimeters	Weight in grams	Date	Snout-vent length in millimeters	Weight in grams
♂	May 11	460	35	June 6	487	40
♂	June 22	423	20	October 15	487	30
♂	June 26	433	23	September 19	500	41
♀	May 11	438	25	August 4	626	80
♀	May 7	495	40	July 11	610	65
♀	May 14	370	18	September 11	646	71
♀	May 7	495	40	June 22	573	55
♀	July 5	508	30	August 6	580	65
♀	July 8	550	61	October 12	630	90
♀	July 2	535	60	August 26	595	55
♀	July 25	537	43	August 18	620	60
♀	May 4	676	92	July 6	730	140
♀	June 20	664	92	August 25	743	100
♀	July 18	623	72	November 11	670	98
♀	July 23	617	83	November 2	680	100
♀	May 11	722	152	August 26	750	120
♀	April 3	748	148	October 21	837	203

August 5—190 millimeters; September 24—256 millimeters; October 10—257 and 300 millimeters. Larger garter snakes also made substantial growth; records of all those recaptured after considerable intervals are shown in Table 6.

Even more rapid gains, sometimes exceeding three millimeters per day, were made by some of the garter snakes at Harvey County Park. Records of seven individuals, all females, selected on the basis of their rapid growth rates, are shown in Table 7.

When the data on snakes recaptured at Harvey County Park are arranged according to sex and size group the snakes are seen to have grown at approximately twice the rate of those at the Reservation. Obviously food was more abundantly available at Harvey County Park, an area of low-lying prairie in sand dunes along the Little Arkansas River. Poorly drained areas among the dunes, which were often flooded with shallow water, provided breeding places for many species of frogs and toads. These amphibians and their tadpoles provided an abundant and varied food supply. Many times in the summer dispersing swarms of newly metamorphosed frogs or toads spread into all habitats. Usually amphibians of various sizes were abundantly available as food. However, at the Reservation the water supply was limited to two small ponds, and two intermittent streams.

Growth in large adult garter snakes was found to be especially erratic and unpredictable. The oldest individuals of a population are probably in most

TABLE 7.—GROWTH IN FEMALE GARTER SNAKES AT HARVEY COUNTY PARK

Original Record			Recapture Record		
Date	Snout-vent length in millimeters	Weight in grams	Date	Snout-vent length in millimeters	Weight in grams
July 5, 1960.....	398	21	August 27, 1960.....	581	65
June 25, 1960....	428	28	October 21, 1960....	687	150
June 15, 1959....	441	35	August 20, 1959.....	676	96
			April 19, 1960.....	703	172
			May 3, 1960.....	725	170*
			August 2, 1960.....	795	150
April 26, 1960....	464	30	October 17, 1960....	771	185
May 28, 1959....	480	50	July 2, 1959.....	574	73
			September 27, 1959..	672	110
June 12, 1959....	537	46	July 23, 1959.....	670	118
June 12, 1959....	578	73	July 16, 1959.....	650	130

* gravid

TABLE 8.—GROWTH IN FEMALE GARTER SNAKES THAT ATTAINED UNUSUALLY LARGE SIZE

Original Record				Recapture Record			
Date	Snout-vent length in millimeters	Weight in grams	Probable age in months	Date	Snout-vent length in millimeters	Weight in grams	Probable age in months
Nov. 14, 1956...	450	29	15	Sept. 28, 1959...	883	215	50
Nov. 11, 1955...	378	16	15	Oct. 8, 1960....	900	410	75
Oct. 16, 1958....	723	170	51	July 30, 1963...	930	290	108
Sept. 2, 1958....	856	255	73	Oct. 10, 1959...	902	227	86
April 13, 1959...	748	148	56	Oct. 21, 1959...	837	203	63
				June 20, 1960...	950	200	71
July 25, 1958...	890	213	?	June 3, 1959....	935	285	?
				May 3, 1960....	940	.....	?

instances near maximum size, and the growth recorded in large adults bears on the problem of longevity. The eleven largest garter snakes captured at the Reservation were all females in the size range 880 to 950 millimeters, and six of them had been captured and marked before they had reached their maximum recorded size. Records of these individuals are presented in Table 8.

The trend of these records indicates that the largest garter snakes at the Reservation, those more than 900 millimeters in snout-vent length, may be as much as nine years old or as little as five years old, but usually are of an intermediate age.

In summary, it may be said that growth in these garter snakes is rapid as compared with growth in most other snakes, but that it is erratic and unpredictable, some individuals gaining more than three millimeters per day in snout-vent length while others remain static. A gain of 1.2 millimeters per day is fairly typical before the rate slows with approaching maturity. In one-year-old males the snout-vent length is usually between 350 and 400 millimeters and subsequently the growth rate slows abruptly. In second-year females the rapid growth rate of the early months is maintained or even increased, although many are already gravid at an age of 21 months. Table 9 based on records of recapture of marked individuals compares the rate of growth (millimeters per month) in snakes of several series, bringing out differences that are caused by sex, size and locality. The largest snakes, females more than 900 millimeters in snout-vent length, grow much more slowly than small or medium-sized individuals, and their rate of growth is even more variable.

TABLE 9.—GROWTH RATES, IN MILLIMETERS PER MONTH, OF GARTER SNAKES IN VARIOUS SIZE GROUPS, AT THE RESERVATION AND AT HARVEY COUNTY PARK

Sex and Locality	Snout-vent Length of Snakes in Sample					
	400 to 449 millimeters	450 to 499 millimeters	500 to 599 millimeters	600 to 699 millimeters	700 to 799 millimeters	800 to 899 millimeters
Males (Reservation)	16.6(10)	7.2(8)	6.6(19)	5.1(7)	.....	.....
Males (Harvey Co.)	50.0(31)	30.0(16)	13.3(15)	7.5(6)	.....	.....
Females (Reservation)	.....	.....	23.4(25)	10.8(34)	9.1(13)	6.3(4)
Females (Harvey Co.)	.....	.....	43.5(10)	24.6(7)	6.7(4)	.....

MOVEMENTS

Carpenter (1952:247) obtained records of 127 movements of the common garter snake at his Cherry Hill study area in southeastern Michigan over a three-year period. The maximum movement recorded was 984 feet and most were less than 600 feet. In general, the snakes tended to stay each in its own small area, which Carpenter termed an "activity range," contrasting this with a "home range" which, according to the same author's definition, must have a home base—a regularly used nest or shelter. No such feature is present in the range of a garter snake. Carpenter noted in those snakes recaptured repeatedly that the pattern of movements tended to have one axis much more elongate than the other. He concluded that the average range is approximately 2.07 acres—600 feet long and 150 feet wide. My own records lead to rather different conclusions which no doubt result from differences in the local populations of snakes, differences arising from field techniques, and differences in interpretation. I suspect the latter two are of greatest importance.

Some of the garter snakes marked and recaptured at the Reservation were at hilltop rock outcrops where it was thought they had come to hibernate, perhaps having travelled beyond their usual spheres of activity. Eliminating these records of the snakes caught at hilltop outcrops, there are available 342 separate records of movements for the snakes on this study area and at Harvey County (Fig. 12).

For a snake recaptured many times at random points, the area encompassed would be sufficiently representative of the home range but would always be somewhat smaller. In actual practice most individuals were caught only once or a few times, and the movements recorded gave little indication of the shape, extent or size of the individual's range. However, in the aggregate the movements measured do reflect the size of the home range. The longest movements probably represent shifts in range, but these are not readily distinguished from movements within a range. *On the average* random move-

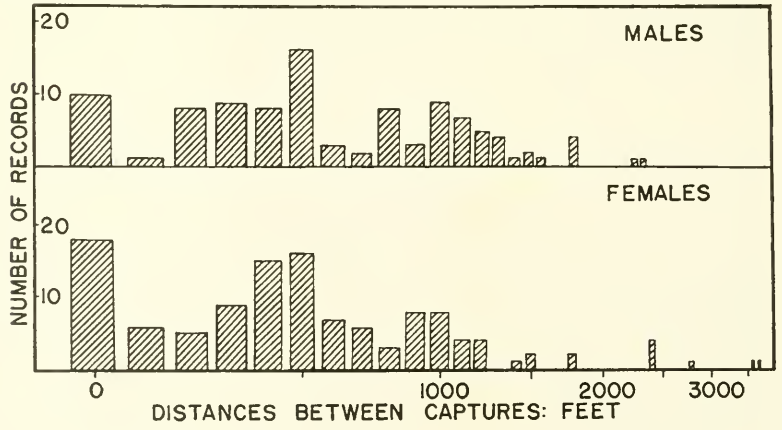


FIG. 12. Movements within or between home ranges in garter snakes at the Reservation and Harvey County Park. Trends are similar in the sexes. Relatively few movements exceed 1250 feet (the approximate diameter of a home range); the longer movements represent shifts in home range.

ments within a home range should be equal to half the range's diameter; some would connect points on opposite edges while others would connect points near together in the central portion. Table 10 shows certain trends revealed by grouping the records of movements according to sex of the snakes involved, according to length of time elapsed between captures and according to locality. Length of movement increases with elapsed time, showing that home ranges are not occupied indefinitely, but either they are gradually altered, or the snakes from time to time shift to new areas abandoning those formerly occupied. The change in time is much more marked in the female garter snakes than in the males, indicating that in the former the home range is altered more rapidly. The females have the smaller ranges. In general, the trends shown by the movements from the Reservation are borne out by the somewhat smaller sample from Harvey County Park.

In Table 10 approximately 20 per cent of each sample, including both the longest and shortest movements were discarded in order to eliminate those that were unrepresentative of home ranges because they resulted from shift of range, and likewise to eliminate movements that were too short to be representative. Some of the snakes were recaptured before they had opportunity to make extensive movements, and certain sites were so favorable that they might yield repeated captures of the same individual, with little or no movement demonstrated, even though the individual had travelled extensively between captures.

Support for the procedure of eliminating the highest and lowest ten per cents of movements recorded is found in the graph of Fig. 13 showing the average movement for 102 females, and the shifting of the average as the extremes at each end of the series are progressively eliminated until only the median remains. The average movement of 554 feet indicates a home range diameter of 1108 feet. Obviously ranges of different individuals are not all

TABLE 10.—AVERAGE DISTANCES IN FEET BETWEEN CAPTURE POINTS OF MALE AND FEMALE GARTER SNAKES FROM RESERVATION AND FROM HARVEY COUNTY PARK, GROUPED ACCORDING TO ELAPSED TIME, SHOWING TENDENCY FOR MALES TO MOVE FARTHER THAN FEMALES AND FOR DISTANCES TO INCREASE OVER LONGER PERIODS

Time	Sex	Reservation	Harvey County	Combined sample
Up to one month	♂	675(for 31 of 38)	719(for 28 of 36)	696(for 59 of 75)
	♀	542(for 60 of 76)	605(for 26 of 32)	562(for 86 of 108)
Two to five months	♂	965(for 13 of 15)	930(for 13 of 15)	920(for 24 of 30)
	♀	814(for 19 of 23)	1047(for 8 of 10)	884(for 27 of 33)
Six to 12 months	♂	753(for 9 of 11)	775(for 11 of 13)	765(for 20 of 24)
	♀	1091(for 25 of 31)	1064(for 9 of 11)	1075(for 32 of 40)
More than 12 months	♂	781(for 8 of 10)	1480(one)	859(for 9 of 11)
	♀	1110(for 15 of 19)	.....	1110(for 15 of 19)

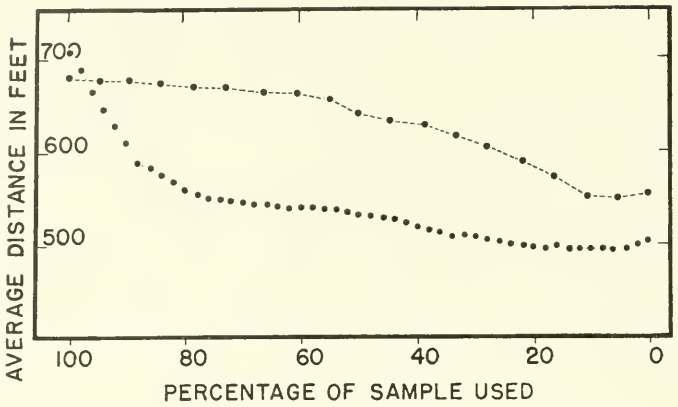


FIG. 13. Diagram showing average movement in 102 female garter snakes from the Reservation (lower line) and 39 males from Harvey County (upper line) and changes in the average as each series is reduced by eliminating the longest and shortest movements in successive pairs until only the medians remain. The series of movements of females included several that were exceptionally long, representing shifts of range. The series of movements of males was more uniform and was less affected by removal of the extremes.

precisely the same size, and though perhaps tending toward circular shape, all deviate in some degree with elliptical or irregular shapes. Therefore, it is to be expected that some movements within home ranges would exceed 1108 feet. The ten longest movements recorded in the series were: 3800, 3560, 3340, 3080, 2720, 2400, 2360, 1920, 1920, 1800. The remaining 92 movements were all less than 1500 feet, hence within the probable limits of a home range.

Assuming that the average figures obtained of home range radius are correct —562 feet for females and 696 for males—and assuming that home ranges tend to be circular, approximate size of the average range may be obtained from the formula πr^2, for the area of a circle. A home range of 35.0 acres for males is indicated, and one of 22.7 acres for females.

In other kinds of snakes also the males have been found to travel more extensively than the females and to have larger home ranges (Fitch, 1958:119; 1960:149; 1963a:391; 1963b:651). Breeding activity probably is not involved because in *Thamnophis sirtalis* mating takes place mainly in a period of a few days after emergence from hibernation, or in autumn shortly before retirement into dormancy, whereas the records that form the basis of my calculations of home ranges are based primarily on summer movements.

In assessing the fact that the home range calculated in Carpenter's study was less than one-tenth of that found in my own study, the sizes of the areas involved must be considered. Carpenter's study area was a rectangle of 48 acres, approximately 1670 x 1250 feet. Nearly one-third of its central portion was rectangular marsh that was little used by the snakes, except along its border where the activity of the snakes and probably that of the collector was relatively concentrated. The maximum possible distance between points

in this area was approximately 2100 feet between opposite corners. Possibly many of the snakes had ranges extending beyond the limits of the study area, although Carpenter did check some of the peripheral areas, and concluded that there was little interchange.

In the part of my own field study carried on at the Reservation a line of 200 live-traps a mile and a half in length and a mile in width at the maximum, was maintained on a study area totalling 750 acres. Ideally traps should have been uniformly spaced in a grid but practical considerations overruled such a procedure, because it was imperative to install the traps where they would be shaded, and where habitat conditions were favorable for the snakes. Actually some degree of randomness was achieved, as the traps were well scattered, and in fact, were set for snakes other than *Thamnophis*, primarily for copperheads from 1949 through 1958 and in the same general area for racers from 1959 through 1962. With the shift in emphasis, from copperheads to racers, no great change in the trap lines or the procedure was involved, but many of the sets were shifted from woodland edge or dense thickets to more open situations in the same general areas. The Harvey County study area was smaller —approximately 4,000 x 2,000 feet.

At the Reservation those snakes caught at rock ledge locations in late September, October or November were thought to be preparing to hibernate. A few of them were caught on either earlier or later occasions in what were presumed to be their summer ranges. Throughout October some garter snakes were caught in the same situations frequented during the summer, and it is uncertain whether all repair to hilltop outcrops to hibernate. Certainly some do so, but others may utilize deep burrows in the meadow habitat where they spend the summer. The 24 females that had made trips between hilltop outcrops and meadows had moved, on the average, 1,745 feet, whereas the corresponding figure for 13 males was 1,138 feet.

Eight males and seven females were each caught twice along hilltop rock outcrops where they were preparing to hibernate in autumn or had emerged from dormancy in spring. One adult female was captured at the same crevice on September 24, 1959, and November 3, 1960. Also, she was captured three times in the summer of 1960 and once in the summer of 1961 in the small valley of the Reservation's headquarters area, and seemingly she had moved some 800 feet up a wooded slope from the nearest part of her home range to reach the hibernaculum. Another female caught at an outcrop on September 28, 1952, was recaptured at part of the outcrop 570 feet from the first location on September 20, 1954. A third female was captured at points 1,320 feet apart, along the ledge on October 27, 1959, and November 3, 1960. A male was caught at rock ledge locations 2,200 feet apart on November 2, 1959, and November 12, 1960. The remaining movements along the rock outcrops were seven for males and five for females. All were for short periods, and averaged 247 feet, indicating some wandering in search of suitable hibernacula even after the snakes had reached the sheltering outcrops.

The records are too few to show the main trend of population movement in connection with dormancy, but do indicate that many, if not all individuals, migrate from their summer ranges in meadow habitat to hilltop outcrops— sometimes only after freezing weather has begun—and that some return to the same hibernacula in successive years whereas others find hibernacula remote from those previously used by them.

DEFENSE AND ESCAPE

In its color pattern *Thamnophis sirtalis* is typical of a large group of colubrid snakes that are active and live in situations having dense ground vegetation. The sharply contrasting colors on the dorsal surface exemplify the "ruptive" type of pattern, breaking up the outlines of the body and hence rendering the animal more difficult to see under some conditions. The longitudinally continuous areas on the dorsal surface serve especially to conceal motion. Ordinarily when a garter snake is seen, part of it is hidden from view by screening vegetation; motion can be readily detected only if the head is in view. Otherwise, as the snake moves forward the section of the body that is exposed seems to shrink and vanish as the observer watches, unaware that it is in motion. In tall grass, or riparian thickets with bramble and nettle these garter snakes are exceedingly elusive.

In day-to-day checking of lines of live-traps on the Reservation I walked scores of miles without seeing a garter snake other than those that were trapped. Those that were seen amid dense vegetation on warm days when they were fully active usually escaped. Often such a snake was barely glimpsed as its initial movement or the slight rustling sound produced drew attention to it. Darting through the dense vegetation with rapid and erratic movements and sudden pauses, the snake usually was beyond danger of capture within a few seconds.

In all subspecies of *Thamnophis sirtalis* occurring to the west of the range of *T. s. parietalis*, the dorsal stripe is especially bright and its edges are so sharply defined that it creates the impression of being painted on the snake. In *parietalis* the stripe is not so bright; it may have a faint suffusion of dusky pigment and the edges are a little less sharply defined. In *T. s. sirtalis* the dorsal stripe is duller, with its edges blending into the adjacent darker areas. *T. s. pallidula* in the extreme northeastern part of the species' range lacks most of the adaptive pattern characteristic of the species throughout the remainder of its range. The dorsal stripe is dull and faint, or absent, and the dorsolateral area is pale, marked with dark spots. Since the range of *pallidula* is entirely within recently glaciated areas, it seems logical to regard its racial characters as recently evolved, and adapted to the special conditions.

Lacking field experience with *pallidula*, the writer is nevertheless impelled to speculate on the adaptive significance of its color pattern on the basis of experience with somewhat similarly patterned

garter snakes of the western United States. In the northern glaciated region inhabited by *pallidula,* summers are relatively cool and snakes must spend a greater part of their time basking in the open in order to maintain body temperatures near their preferred levels; the soil is mostly rocky and ground vegetation is relatively scanty. Against a background of granite boulders, or gravel and sand, the striped pattern would be less advantageous than in dense vegetation, and a pale variegated pattern with spots such as has been developed by *pallidula,* would be more concealing.

Although the garter snake is fast moving and usually is quick to escape at any alarm, it does not always attempt to flee. Instead it may show aggressive behavior with threat displays. The display consists of an extreme lateral flattening of the body and head as the snake coils in readiness to strike, and it may strike if the annoying object comes too near. In the process of flattening, the skin is stretched and the red areas that are mainly confined to loose skin between the scales and are partly concealed at other times, are prominently displayed. The strike is mostly a bluff which in most instances, probably serves to intimidate the enemy rather than to cause any actual injury. I have often teased garter snakes that were engaged in this type of aggressive behavior, and usually the stroke fell just short of a hand presented to the snake at a distance of a few inches, or at the end of a strike the snake's head might touch the hand, but without actually grasping it. The mouth may be opened so widely that if the stroke finds its mark contact with the teeth is unavoidable. Nevertheless there is usually no actual biting and the recoil is almost instantaneous.

Factors that influence the response of the garter snake to threat of danger include type of cover available, type of enemy involved, size and sex of the snake, and temperature. Large garter snakes, especially females, are much more inclined to behave aggressively than are juveniles, and of course this attempt at bluff against a typical garter snake predator, for example a rail or a small heron, would have a much better chance of success. At relatively low temperatures, when the snake is least able to make a speedy escape, it is most inclined to use threatening behavior as an alternative. Captive garter snakes which had become more or less accustomed to handling, and normally evinced no defensive or aggressive behavior, could be caused to flatten, coil, and attempt to strike by cooling them to within a few degrees of freezing.

The defensive display would be least striking in *T. s. pallidula,* in which the flattening of the body and spreading of the skin would

result in little change in the appearance except that the surface area in sight would be increased. In *T. s. sirtalis* the partially concealed markings between the scales are pale, yellowish, greenish or bluish, and provide a far less striking display than the red markings of *parietalis,* at least for those natural enemies that have color perception. Most reptilian and mammalian enemies probably have limited powers to discriminate between colors and do not see red. The displays may be most effective against birds, which have color vision better developed. In *T. s. tetrataenia* of the San Francisco peninsula, having the red markings greatly enlarged and fused into continuous areas, the display is most impressive, and in fact the appearance is striking even when the snake is not engaged in a threat display. Whether the peculiarly striking pattern of *tetrataenia* has any special adaptive value or is merely the chance product of a formerly insular habitat has not been demonstrated. However, potential avian enemies are certainly more concentrated there than over the garter snake's range as a whole. The relatively small range of *T. s. tetrataenia* on the San Francisco peninsula has ocean on three sides, and sea birds, especially gulls, may be seen frequently in almost any part of it. At times these sea birds may resort to freshwater ponds or streams, and could then become a potential threat to garter snakes.

Garter snakes are noted for the nauseous secretion of their anal musk glands. These paired glands are elongate and sausage-shaped and are situated in the base of the tail. The secretion is a tan-colored thick creamy liquid. It is exuded chiefly after the snake has been caught and is struggling to escape. As exudation occurs, the snake presses its vent against the annoying object (or against its own body) and then, with writhing movements, spreads the secretion as widely as possible in a thin film over its own body and that of its captor.

Observations on the effectiveness of the musk glands in deterring attack or ingestion by a natural enemy have rarely been made. On the one hand there is a large body of evidence indicating that many kinds of predators do indeed eat garter snakes despite the musk, but on the other hand most human observers agree that the odor of the musk is highly offensive. Effectiveness of the musk probably depends on the kind of predator and the degree of hunger motivating it, but there can hardly be serious question that the musk does have some deterrent value.

On one occasion when a short-tailed shrew (*Blarina brevicauda*) and a garter snake were caught together in a trap, the shrew

attacked the garter snake at the tail end and ate its way toward the body up to the vent. Along with the remainder of the tail this shrew had eaten the musk glands. However, these glands had doubtless been emptied previously by the snake as it exuded musk in its struggles. On several occasions when predators including raccoons, opossums, and probably skunks, had broken open traps and killed the trapped garter snakes, parts of the snakes, including tail bases with musk glands, had not been eaten but it was uncertain whether these had been discarded because of the musk.

Some of the garter snakes that were handled bit viciously. These were mostly large females. In biting, the snake would deeply embed the long recurved teeth at the rear of the maxillary bone, piercing the skin of a restraining hand in a way that caused profuse bleeding. There is probably some geographic variation in disposition and aggressiveness. My field experience with the more western subspecies, especially *fitchi*, have indicated that these snakes are much less inclined to bite than are members of the subspecies *parietalis*.

A garter snake that has been grasped roughly usually responds by almost instantly voiding the contents of the cloaca, writhing to smear itself and its captor with fecal material and musk. At the same time it twists and thrashes in an attempt to escape. If it is grasped by the tail, it twirls the body rapidly, and within a few seconds may twist the tail off. In garter snakes the tail is remarkably fragile, just as it is in most lizards, and fragility serves the same purpose. When a break occurs, the broken end wriggles about in lively fashion, which might momentarily distract the attention of a predator from the snake itself.

Of 940 snakes examined at the Reservation, 17.9 per cent had incomplete tails, but the percentage was notably different in the sexes: 20.4 per cent in 524 females and only 14.6 per cent in 416 males. In the average male having an incomplete tail, approximately 43.8 per cent of the tail was missing, whereas in the average female the corresponding figure was approximately 50 per cent. The larger snakes, on the average, had more injuries to the tail, and also tended to have more of the tail missing. In males the incidence of incomplete tails was: eight per cent in those of 300 to 400 millimeters (snout-vent), 11 per cent in those of 401 to 500 millimeters, 22 per cent in those of 501 to 600 millimeters, and 24 per cent in those of 601 to 700 millimeters. In females the corresponding figures were: 7, 12, 16, and 25 per cent; 30 per cent in those 701 to 800 millimeters and 41 per cent in those more than 800

millimeters. Hence, the greater incidence of tail injuries in females seems to be correlated with their greater bulk rather than with any difference between the sexes in habits. The larger and heavier snakes when grasped by the tail, can snap or twist it off more easily than can smaller and lighter individuals.

NATURAL ENEMIES

In 1952, 1955, and 1958 through 1963, pellets of the red-tailed hawk (*Buteo jamaicensis*) were collected in early summer from beneath nests whenever the opportunity arose. Several of the nests were on the Reservation and Rockefeller Tract; a much larger number were at localities well scattered throughout the eastern part of Kansas. In the total of 1320 pellets examined there were exactly 100 occurrences of the garter snake, which was hence a fairly important component of the food, although it ranked behind the cottontail (*Sylvilagus floridanus*), the prairie vole (*Microtus ochrogaster*), the cotton rat (*Sigmodon hispidus*) and the black rat snake (*Elaphe obsoleta*). In a collection of 116 red-tailed hawk stomachs donated by the U. S. Fish and Wildlife Service from localities well scattered throughout the United States and southern Canada, there were 152 vertebrate prey items of which three were *Thamnophis sirtalis:* one from Shoal Lake, Manitoba, May 30, 1917; one from Oak Lake, Manitoba, October 2, 1921; and one from Lac de Nonne, Alberta, May 26, 1926. Another occurrence listed merely as *Thamnophis,* from Norwich, Connecticut, also may have been this species.

In a smaller series of broad-winged hawk (*Buteo platypterus*) stomachs received from the U. S. Fish and Wildlife Service, there were three occurrences of natricines, some or all of which may have been the common garter snake. Twenty-five pellets collected beneath the nest of a Swainson hawk (*Buteo swainsoni*) in July, 1962, in Miami County, Kansas, approximately 30 miles southeast of the Reservation, contained 57 prey items of which 6 were *Thamnophis,* presumably the present species. Guthrie (1932:102-103) mentioned instances of predation on *Thamnophis sirtalis* by Swainson's hawk, the sparrow hawk (*Falco sparverius*) and the Virginia rail (*Rallus virginianus*).

Randall (1940:166) recorded garter snakes in the food of Pennsylvania marsh hawk. Conant (1951:253) mentioned the finding of a garter snake in the stomach of a red-shouldered hawk in Montgomery County, Ohio, and Ernst (1945:453) in New York found

garter snakes and water snakes to constitute approximately three per cent of the food at the nests of 16 red-shouldered hawks. In Minnesota, Errington and Breckenridge (1938:113-121) recorded garter snakes in the food of the red-tailed hawk, broad-winged hawk, and Swainson's hawk. Even the ruffed grouse has been recorded preying upon garter snakes (Zorichak, 1953:2).

Among mammals, raccoons, skunks, minks, foxes and badgers probably include the most important predators on the garter snake over its range as a whole. Unfortunately, workers who have studied the food habits of these animals have usually tended to lump garter snakes in such broad categories as "reptile" or "snake," or at least have failed to distinguish species, so that the extent of predation on *Thamnophis sirtalis* is difficult to judge. Because of the small size of the newborn snakes, relatively small birds and mammals, which are not normally predators on other vertebrates, may occasionally eat them. McKeever (1958:170) recorded an instance, observed near Peterborough, Ontario, in which a chipmunk (*Tamias striatus*) attacked a 14-inch garter snake. The snake was said to be slow and sluggish, presumably because of cold weather, as the date was April 20, 1957. The chipmunk dragged the snake into a hollow log as the observer watched. The snake was still writhing feebly, but when it was examined was found to be helpless, its head chewed to a pulp. As the observer left, the chipmunk returned to the attack. Even a "mouse" (*Microtus* sp.?) has been observed to make an unprovoked attack on a small garter snake.

In the course of my study at the Reservation and Harvey County Park 1339 food records of the blue racer (*Coluber constrictor*) were accumulated, and 18 of these were garter snakes. Except for the relatively minute insect items, chiefly crickets, grasshoppers, and katydids, the garter snake was actually one of the more frequently occurring items, exceeded among vertebrates only by the six-lined racerunner (*Cnemidophorus sexlineatus*), prairie vole (*Microtus ochrogaster*), and wood mouse (*Peromyscus leucopus*). Other records of the racer preying upon this garter snake include those of Taylor (1892:330), Surface (1906:170), Ortenburger (1928:181, 228), Breckenridge (1944:118), Finneran (1948:124), and Duellman (1951:338).

There is circumstantial evidence that other predators, for which no records were obtained, may have taken even heavier toll of garter snakes on the area. On numerous occasions the wire funnel traps in which most garter snakes were caught were disturbed by

mammalian predators, but the type of disturbance varied. Sometimes the trap had been merely rolled or pushed away from its position, but remained unopened, either with or without a trapped animal. In other instances the trap had one end, either the funnel entrance or the plug at the rear, wrenched away, or mashed and collapsed on one side permitting the predator to gain access to the animals caught. In still other instances, when the trap could not be opened a paw had been inserted through the funnel entrance and the trapped animal had been removed, sometimes only after a violent struggle, when the inserted paw had become snagged on the inward-projecting wire prongs of the funnel. Mammals known to have disturbed the traps from time to time include domestic dogs, raccoons, opossums, skunks (both striped and spotted) and long-tailed weasels. In many instances the evidence was insufficient to identify definitely the predator involved, but raccoons were known to be the most habitual and skilled raiders of the trap lines. Most often insects, small mammals, or frogs were the prey sought from the traps, but on several occasions remains of garter snakes that had been removed from the traps and partly eaten were found nearby. Garter snakes in traps were seemingly more subject to attack than were some other larger and more formidable kinds of snakes, such as the copperhead and black rat snake, and probably they are occasionally caught and eaten under natural conditions by each one of the mammalian predators mentioned.

At the pond on the Reservation green herons (*Butorides virescens*) were often present in spring, and great blue herons (*Ardea herodias*) often visited both this pond and the smaller one on the Rockefeller Tract. Both may have caught garter snakes. The numerous large bullfrogs present at both ponds also were potential predators on small garter snakes that ventured into the vicinity.

Although many records are available of mammalian, avian and reptilian predators feeding upon *Thamnophis sirtalis,* the role of predation in general or of any one predator species in regulating its populations are still unknown. Even less is known about mortality in hibernation, or from drought, or disease.

PARASITES

The only ectoparasites observed on the garter snakes of my study areas were chiggers. These larval mites varied greatly in abundance according to the time and place. Abundance was greatest in hot, humid weather of early summer in moist situations with mesic vegetation. The garter snakes handled usually were not thoroughly checked for chiggers, but in early summer most individuals carried them. Sometimes many hundreds were attached to one snake, their close-packed bodies forming a reddish encrustation

over the loose skin between the scales. Even with such heavy infestations the snakes suffered no visible ill effects.

Loomis (1956) made an intensive field study of chiggers from 1948 to 1952, which was most concentrated on the Reservation, but included many areas in other parts of Kansas and in neighboring states. Of the many species present on the Reservation, he found only three attached to garter snakes: *Trombicula alfreddugési* (1596 individuals), *T. lipovskyana* (40 individuals), and *T. kansensis* (4 individuals). *T. alfreddugési* is the common pest chigger that attacks humans; it is remarkably catholic in its choice of hosts, utilizing many species of mammals, birds and reptiles, and occasionally certain amphibians. *T. lipovskyana* is a less common species that is similar in its ecology. *T. kansensis* is a member of a different subgenus. It is known from only a few localities, chiefly from relatively dry and rocky habitat, and deer mice (*Peromyscus maniculatus*) are the most frequent hosts, but the chigger has been found also on four species of snakes, including *Thamnophis sirtalis.*

Styphlodorine trematodes, so-called lung flukes, are found in many kinds of snakes including garter snakes. Insofar as known all members of this group have in addition to the vertebrate host of the adult, intermediate hosts for the developmental stages—first a water snail and then a frog. The eggs escape through the digestive tract of the snake and in aquatic situations hatch producing free-swimming larvae which to develop further must find the right kind of snail and embed themselves in its tissues. After completing this phase of its development the parasite produces asexually numerous free-swimming larvae of a second type. These parasitize tadpoles, remain in them after the tadpoles metamorphose, and complete their development only when the frog is eaten by a snake.

In keeping with its liking for wet places and its frog-eating habits, *Thamnophis sirtalis* is a frequent host of various styphlodorine flukes. Kinds recorded in the literature as having been found in *T. sirtalis* include: *Dasymetra longicirrus, Lechriorchis insignis; L. plesientera, L. primus, L. tygarti, Ochetosoma megametricum, Zeugorchis aequatus, Z. curinus,, Z. megacystis, Z. syntomentera,* and *Z. syntomenteroides.* In the summer of 1958, Miss Peggy Lou Stewart checked many of the garter snakes caught on the Reservation and Rockefeller Tract for flukes. She found that most of the snakes caught in June and July had *Zeugorchis megacystis* in their mouths and gullets. In other months flukes were rarely found, but they may have been present farther down the digestive or respiratory tracts where they could not be seen without sacrificing the snake. Miss Stewart examined 326 garter snakes (*T. sirtalis, T. radix* and *T. proximus*) in the University of Kansas Natural History Museum, from localities in various parts of Kansas. Six of these preserved snakes of all three species had *Zeugorchis megacystis* in their lungs. This fluke is about 2.5 millimeters long with body .7 millimeters wide, and attenuate anteriorly (Stewart, 1960).

None of the live garter snakes that were found to be infested with *Z. megacystis* showed any pathologic effects. In November, 1963, a large female *T. sirtalis* that had been in confinement several weeks, but had refused food and was of emaciated and sickly appearance, was found to have many flukes in its mouth. These were identified by Dr. William H. Coil as *Zeugorchis syntomentera.*

COMPOSITION OF THE POPULATION

In nine broods born in captivity to females from the Reservation and Harvey County Park, there were 68 males and 53 females, but the sample is too small to permit much confidence in the 1:.78 male-female ratio, or even to indicate that males are more numerous than females in broods. In southeastern Michigan Carpenter (1952:253), with a larger sample of 360 young from 20 broods, found a male-female ratio of 1:.91. The trend of the figures indicates that males are slightly more numerous than females at birth.

In adult garter snakes the sex ratio in samples varies according to the season. In 519 snakes of my autumn sample from the Reservation, representing the combined data of 15 years of trapping, there were 301 males and 218 females. The 1:.72 sex ratio is probably distorted. In autumn there is some sexual activity; hence females caught in traps may serve as bait to attract males. Often a pair was found in a trap, and occasionally one female was accompanied by several males.

In late spring and summer, however, the sex ratio of trapped samples cannot be influenced by sexual attraction, since sexual activity wanes rapidly after a short and intensive breeding period immediately after emergence from hibernation in early spring (ended before trapping began). The totals for the several years of trapping from May through August were: males—154, females—254. Many of these were second-year individuals, which in spring and early summer were still adolescent, and often were still small enough to pass through the quarter-inch wire of the traps. In this respect the traps were probably somewhat selective, because adolescent males, lagging behind the females of the same age in their growth, would be able to escape from the traps after the females were too large to do so. To avoid the bias arising from this selectiveness, all those snakes of both sexes known or supposed to be second year individuals were eliminated. There remained 255 adults, third year individuals or older, of which 99 were males and 156 were females. The 1:1.58 sex ratio indicated by these figures may be somewhere near the correct one, but probably there are various distorting factors. The home ranges of males, more than 50 per cent larger than those of females according to my calculations, would cause males to be caught oftener and in more traps than their female counterparts. Hence, males may be even less numerous than the ratio of actual captures indicates.

Age structure of the population was calculated from a combination of the records of marked individuals recaptured and the size distribution of all the snakes captured. Each individual recorded was assigned to an age group, either on the basis of its known growth, if it had been recaptured, or arbitrarily on the basis of its size if actual growth records for it were not available. In summer, individuals late in their first year or early in their second year were in many instances too small to be held in the traps and therefore were not adequately represented. The sample used is therefore that drawn from fall and spring, when the second-year snakes are nearly all large enough to be caught. The distribution of 650 adults according to age and sex is shown in Table 11.

The trend of figures in Table 11 suggests that in adult garter snakes of the population studied there is an approximately 50 per cent loss from one year to the next in any age group. The rate of loss is not detectably

TABLE 11.—NUMBERS AND PERCENTAGES OF ADULT GARTER SNAKES IN DIFFERENT AGE GROUPS IN A SPRING AND FALL SAMPLE

Age Group	Both Sexes Combined		Females		Males	
	Numbers	Percentages	Numbers	Percentages	Numbers	Percentages
second year	323	49.7	153	50.1	170	49.9
third year	162	25.0	69	22.6	93	27.0
fourth year	97	14.9	40	13.1	57	16.5
fifth year	34	5.2	17	5.6	17	4.9
sixth year	17	2.6	14	4.6	3	.9
seventh year	11	1.7	9	2.9	2	.6
eighth year	6	.9	3	1.0	3	.9
Totals	650	100	305	100	345	100

different in males and females. In a cohort of 100 second-year individuals the life expectancy is such that typically only one or two would survive into their ninth year. The rate of attrition seems to be neither slowed nor increased with advancing age.

Actually, snakes more than five years old were caught in such small numbers that chance played a major part in their distribution and it is uncertain whether the rate of loss characteristic of the younger adults was still maintained. Senility theoretically might be a factor in the dying off of the oldest snakes, but no evidence of it was noted. All of the largest and oldest garter snakes examined appeared healthy and vigorous. Their large size, especially in the females, would seem to confer a distinct advantage in defense against certain natural enemies.

In calculating the productivity of a population it must be taken into account that the adults comprise at least seven discrete annual age classes, each class with a different number of individuals and differing somewhat from all the other classes in fecundity. Some of the younger adult females do not ovulate, and those that do produce fewer ova than older adults. Table 12 has been compiled with attempt to allow for these differences between age groups, though admittedly the data on which it is based are imperfect and almost surely the trends would be altered somewhat with larger samples.

Actually the number of young produced by the cohort considered in Table 12 would be fewer than 776 because some of the females would be eliminated by natural causes before the time of parturition, and of those that survived some would lose fetuses by abortion or resorption, or death at the time of birth. In the absence of evidence to the contrary, it must

TABLE 12.—THEORETICAL PRODUCTIVITY IN A COHORT OF 100 ADULT FEMALES IN EARLY SUMMER

Age group	Percentage of adult female population	Percentage of gravid individuals in age group	Number gravid	Number of eggs per female	Number of young produced
second year.....	50	42	21.0	11.4	240
third year.....	25	58	14.5	12.3	178
fourth year.....	12.5	92	11.5	16.0	184
fifth year.....	6.25	92	5.75	15.7	90
sixth year.....	3.12	100	3.12	15.5	48
seventh year.....	1.56	100	1.56	15.5	24
eighth year.....	.78	100	.78	15.5	12
Total.....	100	.....	58.21	13.33	776

be assumed that the mortality rate is uniform throughout the year, and if this is true the cohort would sustain a loss of near ten per cent during approximately ten weeks of gestation, reducing the estimate of 776 young to only 698. In those females surviving to parturition a further ten per cent reduction may be conservatively estimated from infertile eggs and from embryonic and fetal mortality during development and at the time of birth. Consequently the number of live young produced might be in the neighborhood of 628.

The rate of loss by natural causes in juveniles is almost certainly higher than the rate of loss in adults, and the smaller the young the more rapid would be the expected death rate. If the male to female ratio at birth is 1 to .9, the 628 young would include 297 females, and in a 21½-month period these would be reduced to 50. If there is a 64 per cent reduction in the first-year young, leaving 107 surviving one-year-olds, and if these are subject to a further 53 per cent reduction in the following nine and a half months, the requisite number of breeding second-year females (50, replacing the second-year females in the original cohort of 100) would be obtained.

In summary, a cohort of 100 adult females in May might be reduced to 90 by early August, but by then they would have given birth to about 297 female young, and there would then be also about 107 one-year-old female survivors from the previous year's brood. Calculation of the number of male counterparts represented by these females is probably subject to a wider range of error. There would be about 331 newborn males; about 57 adult males (accepting the 1:1.58 ratio indicated by trapping as correct), and perhaps 107 one-year-old males. According to my calculations the population is increased by about 173 per cent at the time young are born.

NUMBERS

From 1949 through 1957 the garter snakes recorded in my study were essentially those trapped along hilltop limestone outcrops in autumn, with a relatively small number caught in summer. However, for the last six years of the study, 1958 through 1963, extensive summer trapping was carried on, and the catches of adult snakes at locations away from the rock outcrops, were as follows: 49 in 1958, 173 in 1959, 153 in 1960, 152 in 1961, 81 in 1962 and 72 in 1963. These figures do not satisfactorily reflect the actual numbers present. Both trapping effort and the area covered by the trap lines differed somewhat from year to year. The majority of individuals recorded were caught only once, and new individuals continued to be caught, throughout the course of the study; therefore it was obvious that most of the population had not been included in the samples.

Under these conditions "census" could be carried out only by obtaining a ratio within a given period of individuals previously caught and those captured for the first time. Snakes are not especially well adapted to census by the "Lincoln Index" method. Secretiveness, seasonal changes in habits, and differences in behavior between the sexes are all complicating factors. The relatively long time required to capture snakes in sufficient numbers for a sample is a serious drawback of the method; in the period of weeks or months usually required the population is changed by immigration, emigration, reproduction and mortality.

Each year's data were used as a separate unit in my census computation. Obviously in the period May through November some shifting of individuals occurred. This would constitute a source of error; some marked individuals would have moved out of the study area while others moved in. Underrepresentation of marked individuals in the later samples would result in an erroneously high figure being obtained for the total population present. While this factor undoubtedly influences the results and increases their margin of error, its effect must be relatively minor, because study of the records of movements of individuals has shown that most maintain home ranges and stay in the same small area over periods of months.

The capture-recapture census involves two sampling periods—a preliminary period in which a number of the animals are caught and marked, and a follow-up period in which the ratio of those previously marked to others is determined. An entire summer's records could be divided in various ways, and many different figures could be obtained for essentially the same population. In my census computations the season's records were divided into monthly units. In 1959, for instance, 24 snakes were caught and marked in the month of May. In June 37 were caught of which 5 were recaptures from the original group of 24 marked in May. The total population (P) present on the study area in May is indicated by the formula $\frac{P}{24} = \frac{37}{5}$ or $P = 178$. In July 40 snakes were captured of which two were among the 37 recorded in June. Hence, for June $\frac{P}{37} = \frac{40}{2}$ or $P = 740$. Similarly the July catch, on the basis of August recaptures, indicates a population of 252, and for August and September, figures of 646 and 273, respectively, were obtained. Actually the

population of June was the same as that present in May minus the small percentage that had been eliminated through natural causes in the interval. Each month's census figure should have indicated a slight decline from that of the previous month if the figures had been highly accurate, but no such trend was evident, and a wide range of fluctuations results from the small size of the samples. The average of all five samples was 422, and this figure is probably more nearly correct than any of the separate census computations.

If periods longer than a month are used as sampling intervals, more substantial numbers of recapture records are usable in the computations. For instance, of the 24 snakes caught in May, 1959, nine were recaptured along with 149 new snakes in the period June through October, and the formula may be stated: $\frac{P}{24} = \frac{158}{9}$ or $P = 421$. Or the preliminary period used may be May-June and the follow-up period July-August-September-October resulting in a slightly changed ratio as follows: $\frac{P}{56} = \frac{131}{14}$ or $P = 524$. With preliminary periods successively lengthened to May-June-July, May-June-July-August, and May-June-July-August-September and with the follow-up period in each instance consisting of the remainder of the growing season, through October, separate census figures of 531, 504, and 422 were obtained. For this whole series of five censuses there was a total of 66 recapture records, against only 16 from the same set of data divided into one-month census intervals as in the preceding paragraph. For the longer periods the average of five capture-recapture censuses was 480, with a markedly smaller deviation than was obtained with the shorter census periods and fewer recaptures. The smaller deviation indicates that for the longer periods more adequate samples were obtained. But the increased interval also allows more time for disappearance of the marked snakes, and the relatively high census figure may reflect error due to this factor.

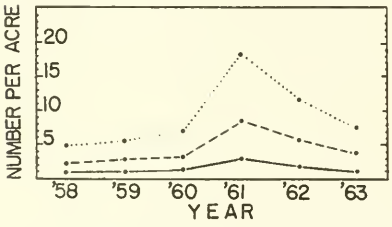


FIG. 14. Diagram showing population density of garter snakes calculated for the Reservation study-area by Hayne method of capture-recapture census. Lower line shows population of adults in early summer of each year calculated from actual "census." Middle line shows numbers estimated to have been present in early summer, making allowance for the juveniles that were not caught in the traps; upper line shows numbers estimated to have been present in late summer at time of annual maximum after birth of young.

In Lincoln Index censuses it is commonly observed that those computations based on only one recapture or a few, are subject to wide fluctuation, while computations based on more recaptures tend to fall within an expected range. Therefore, in averaging several such census computations it seems a reasonable procedure to weight each one according to the number of recapture records on which it is based. The weighted average for the five 1959 censuses, based on a total of 66 recaptures, as explained in the preceding paragraph, is 492.

A refinement of the Lincoln Index method of census since it was proposed by Hayne (1949:399) has been widely used by vertebrate zoologists. In this method a series of population computations is made; in the case of my 1959 data the May population was computed from the capture-recapture ratio in June; the May-June population was computed from the ratio in July, and so on. With successive census samples the ratio of recaptures steadily rises, as the pool of marked individuals grows. By projecting the trend of these increasing ratios the total population can be estimated. The actual procedure is rather involved and will not be explained in detail here; the reader is referred to the original publication, for a fuller explanation of the procedure and mathematical theory. For my 1959 samples the ratios of recaptures to total captures in June, July, August, September and October, respectively, were 8.2, 11.6, 28.6, 20.0, and 39.3 per cent, and the total number of snakes indicated was 357.

Still another method of using the Lincoln Index consists of combining the figures from several separate sampling periods before the census computation is made. Thus for the summer of 1959 in five preliminary sampling periods (May, May-June, May-June-July, May-June-July-August, May-June-July-August-September) there were caught 24, 56, 94, 124, and 156 snakes, totalling 454, and in the five corresponding follow-up periods there were caught 158, 131, 96, 65 and 7—totalling 477, with recaptures 9, 14, 17, 16 and 10, totalling 66. Hence, $\frac{P(5)}{454} = \frac{477}{66}$ or $P = 656$.

All four of the census methods described above are included in Table 13 for the sake of comparison. The Hayne method is probably the most reliable and in most instances, but not all, it yielded the lowest census figures.

TABLE 13.—POPULATION OF ADULT GARTER SNAKES ON RESERVATION STUDY AREAS CALCULATED FROM CAPTURE-RECAPTURE DATA BY FOUR DIFFERENT METHODS

Year	Number of snakes in census samples	Number of recapture records*	Estimated acres in area sampled	Estimated numbers of snakes			
				Hayne method	Average of means	Weighted average	Average of combined samples
1958	49	3	324	268	290	287	413
1959	173	44	374	357	480	492	656
1960	153	28	374	435	888	676	761
1961	152	10	324	993	1427	1035	1208
1962	81	9	176	345	284	285	324
1963	72	14	176	222	189	186	211

* Recapture records within the same month are not included, nor are those of snakes from any previous years.

In all four methods, the trends for the six-year period are similar, and indicate great changes in the number of snakes from year to year. Beginning with a relatively low population in 1958 the numbers increased steadily through 1961, with the greatest gain coming from 1960 to 1961 and more than doubling the population in a year. In the last two years the trend was reversed, with an even more rapid decrease, and in 1963 the population had decreased to a level even lower than that of 1958 (Fig. 12). Drastic changes in population level from year to year are to be expected in species like this garter snake which have a high reproductive potential, with large broods and with a fairly short time (two years at the minimum) between generations. Klimstra (1958:232) presented figures intended to show "cyclic" changes in populations of snakes, but his evidence was not entirely convincing because data for several species and genera were combined and data for part of the period of his observations originated from Iowa, the remainder from Illinois. In any case Klimstra's data did not afford evidence of a regular cycle, but merely of rather large changes in numbers from year to year, with progressive trends continuing over several years.

In the garter snakes of the Reservation population changes are probably controlled by a complex combination of factors, and the available records of weather and of associated animals provide few clues as to causality. It might be expected that the food supply would be one of the most critical factors, but food supply is in turn largely controlled by the weather. Ample and well distributed rainfall would seem to render conditions favorable to garter snakes, partly by promoting the development of lush vegetation for shelter, but especially by promoting the successful reproduction and dispersal of the leopard frog and other important prey species. Although the figure for the annual total of rainfall might have some significance, the seasonal distribution is more important. Precipitation during the time of year that the snakes are hibernating affects the snakes by replenishing the water supply of creeks and ponds, but precipitation during the warmer half of the year, when the snakes are active is much more critical. Especially after birth of the annual crop of young, in late July and early August, precipitation must be adequate in amount and well distributed for the small garter snakes to thrive. Available records indicate that earthworms are the most important food, but in dry weather such as that in August, September and October of 1953 earthworms are usually well beneath the soil surface, out of reach of the young snakes, which, as a result are undernourished and presumably die off faster than they

TABLE 14.—PRECIPITATION (IN INCHES) ON THE UNIVERSITY OF KANSAS NATURAL HISTORY RESERVATION IN WINTER, EARLY SUMMER, AND AUTUMN OF SIX DIFFERENT YEARS

	1958	1959	1960	1961	1962	1963
November through April....	14.72	14.14	12.14	16.79	14.09	5.47
May-June-July.....	21.61	10.59	10.38	13.95	14.36	11.06
August-September-October..	9.69	15.39	8.76	17.33	14.85	6.11

would under more favorable conditions. The peak population of garter snakes present in 1961 consisted mostly of young adults, born in the summer of 1959. Rainfall in August, September and October, 1959, totalled 15.39 inches, more than for the corresponding periods of most other years, and those young snakes that were recorded had made unusually rapid growth. In the autumn of 1961 precipitation was even higher, but by 1963 the population had decreased as a result of other, unfavorable factors. Seasonal precipitation for six different years at the Reservation is shown in Table 14.

SUMMARY

Over a 15-year period, 1948 through 1963, a population of the garter snake, *Thamnophis sirtalis parietalis,* was studied on the University of Kansas Natural History Reservation, the northeasternmost section of land in Douglas County, and from 1958 through 1963 on the adjacent Rockefeller Experimental Tract, a quarter-section in Jefferson County. An equally intensive field study was carried on 140 miles to the southwest at Harvey County Park, 1959 through 1963.

The populations studied were near the center of the species' geographic range, and were typical of the subspecies *parietalis.* Adult females ranged from 504 millimeters (snout-vent) and 21 grams to 950 millimeters and 410 grams, and adult males ranged from 387 millimeters and 14 grams to 678 millimeters and 110 grams. Newborn young typically are about 168 millimeters and 1.9 grams. The relatively small size of newborn young is correlated with large litters and high infant mortality.

The range of the species is more extensive than that of any other American snake, and includes much of North America except for its arctic and tropical portions. Over this large area the garter snake is represented by 11 named subspecies. There is notable stability geographically in numbers of body scale rows, numbers of labial scales, and perhaps in body size, although these characters are highly variable in some other species of garter snakes. Geographic variation is striking in the color, width and distinctness of the dorsal stripe and lateral stripes. The dorsal stripe especially is usually bright yellow contrasting with the dark color of adjacent areas, occupying the middorsal scale row and half of each adjacent row. But in *sirtalis* and *pickeringi* the stripe is reduced and in some individuals of *pallidula* it is absent. In most subspecies the dorsolateral area of each side is dark, almost black, but is notably paler in *sirtalis, pallidula, ornata* and *infernalis.* Pale crescent-shaped flecks confined mainly to loose skin between the scales and arranged in several

longitudinal rows, are yellowish, greenish or bluish in the more eastern subspecies, but in *parietalis* at least the lower rows of flecks are usually some shade of red, and all the more western subspecies have red in the pattern. When the snake is cornered or captured the red marks are most prominently displayed. Lateral stripes are narrower and duller than the dorsal stripe and they may be broken by dark marks as in *semifasciata* or may be obscured or altogether lacking in the somewhat melanistic *concinnus* and *pickeringi*. These same two subspecies are heavily marked with black ventrally, but most others have whitish chins blending to pale blue or green (sometimes tinged with red) farther posteriorly on the ventral surface. The pattern with longitudinal striping in contrasting colors has adaptive value; it effectively conceals motion in the habitat of dense vegetation where the snakes are usually found.

In its habits and habitats *T. sirtalis* is fairly typical of its genus. Almost everywhere that it occurs (except in the far north) it is sympatric with more specialized competitors of the same genus which must sometimes place a heavy strain on its resources. In the eastern half of the United States *T. sirtalis* is characteristic of dense vegetation in mesic habitats. On my study areas it was most often caught in tall prairie grass or in brush. However, farther west it is increasingly confined to marshland or other riparian situations. Compared with other snakes, the common garter snake is exceptionally cold-hardy, and can survive temperature as low as —3° C. Some remain active until after the advent of freezing weather in autumn and emerge relatively early in spring. They are active over a wide range of air temperatures, but seem to prefer a bodily temperature between 29° C. and 30° C. The critical thermal maximum is near 41° C.

Amphibians (chiefly frogs) and earthworms make up most of the food. In my field study 200 food records were obtained. The leopard frog was locally by far the most important food species, with 120 recorded occurrences. There was a variety of other salientians (ranid, hylid, bufonid, microhylid), 5 earthworms, 6 cricetid mice, 2 voles, 1 bird and 1 snake (juvenal copperhead). Earthworms are especially important as food for the first-year young, whereas adult frogs and miscellaneous other vertebrates are eaten chiefly by large garter snakes.

Composition of the food varies greatly from time to time and place to place, depending on the relative availability of the favorite types of prey. The supply of earthworms, and frogs (mostly immature), which are the chief food sources, are subject to consider-

able fluctuation. Growth rate of the snakes is hence subject to much variation. Some young make little gain by the time of their first hibernation in late autumn and presumably most of these do not survive. A gain of approximately 1.1 mm. per day in snout-vent length is most typical for this autumn period. In the following growing season the rate is usually a little more rapid. By mid-June a typical first-year garter snake has more than doubled in length, measuring approximately 380 millimeters and weighing about 14 grams. At this age males and females have diverged but little in growth, but by then the males are approaching sexual maturity and slow their growth abruptly. By autumn, at an age of 15 months, they average about 455 millimeters in snout-vent length, whereas females of the same age having continued their early rapid growth, have reached approximately 550 millimeters, on the average.

Although daily length increments of 1.1 to 1.3 millimeters per day are most typical for growing young, some thriving individuals grow at more than twice this rate for periods of weeks or months. Other garter snakes of all sizes fail to make any gains over periods of months. Growth rates are especially depressed in drought summers when food is scarce. On the Reservation the largest garter snakes (all females) from 900 to 950 millimeters in snout-vent length were from five to nine years old, according to growth records available for some of them.

In *Thamnophis sirtalis* there is sporadic sexual activity after the onset of cool weather in autumn, and there is a more concentrated breeding season in early spring. Copulation occurs chiefly on the first warm day of spring that the snakes are active, and sexual activity wanes rapidly. The males carry on active sexual search and females are found mainly by scent. The female's role in mating is almost entirely passive, and it is not known whether she has a definite oestrus period. Sexual relations are promiscuous, and several or many males may simultaneously court the same female. Typically she is larger than any of her suitors. The male lies on the female, or alongside her, with rhythmic writhing movements, his cloacal region pressed against hers. When intromission has been attained, the male's movements cease and he is dragged behind the female for periods of minutes as she moves about slowly. Males have been known to breed with several females in succession. Usually as copulation begins the unsuccessful suitors disperse. Congealed semen distends the female's cloaca after mating, and may function as a copulatory plug.

Ovulation occurs many weeks after insemination, in May. Palp-

ing of 132 gravid females on my study areas indicated an average of 14.5 eggs. Some of the eggs—an estimated 4.6 per cent—are lost during pregnancy. Number of young is closely correlated with size and age of the female, and varies from an average of 12.0 in two-year-olds to 16.8 in four-year-olds. Furthermore less than half the two-year-olds produce eggs, but 100 per cent of those examined that were six years old or older were fecund. An extensive literature indicates that occasionally litters are much larger than those recorded by me, with a maximum of more than 80 young. Undue attention to unusually large litters has resulted in bias toward abnormally high figures in the literature. Zehr (1962:324) found (by dissection) an average of 12.9 embryos in 104 gravid females from New Hampshire, by far the largest series yet recorded.

The average distance between successive captures, 696 feet for males and 562 feet for females, were interpreted as representing home ranges of 35.0 and 22.7 acres respectively. All these movements were for relatively short intervals, one month or less. For longer intervals distances were greater showing that home ranges are not necessarily permanent but may be altered with time. On the Reservation many or all of the garter snakes made migrations from their summer ranges to hilltop limestone ledges where deep clefts and crevices provided abundant hibernacula. Several such movements were in the neighborhood of a quarter mile. Insofar as known, individuals did not return to the same hibernaculum or to the same area of ledge in successive years.

The striped pattern of *Thamnophis sirtalis* is highly effective for concealing motion; the snake is capable of rapid movement and is elusive in its normal habitat of dense vegetation. When unable to make its usual rapid getaway, a snake slowed by low temperature or cornered, may resort to bluff, coiling, flattening the body, displaying conspicuously the red markings between the scales, and striking. If restrained, it may deliver a painful bite and further discourages a predator by smearing its own body and that of the captor with feces and musk. A garter snake that is inadvertently grasped too far posteriorly will adroitly twist off the tail and while the latter performs lively wriggling movements distracting the captor, the snake itself may escape. As a result of such incidents incomplete tails were common in the populations studied, especially in large adults.

Important natural enemies include the red-tailed hawk (100 garter snake occurrences in 1320 pellets), Swainson's hawk (6 garter snake occurrences among 57 prey items), blue racer (18 garter

snakes among 1339 food records), raccoon and opossum. Hawks, water birds and carnivorous mammals certainly include some of the chief natural enemies of the garter snake throughout its range, but their effects on populations are not known and there is little evidence as to what factors actually control populations. At least three species of chiggers and two species of lung flukes parasitize the local populations of garter snakes studied. At least nine other kinds of lung flukes have been found in *Thamnophis sirtalis* from other localities. None of these parasites produces any obvious ill effects in the snake host.

In the adult population studied, males were less numerous than females, in a ratio of .61 to 1. The adults represent at least seven annual age groups. Typically from one year to the next a cohort of adults is reduced by approximately 50 per cent by natural mortality factors. Seemingly the rate of mortality changes little with increased age and size. Because of rapid population turnover and lack of efficient means for capturing the snakes a majority remained unmarked even after many years of field work on the areas most intensively studied. "Census" therefore had to be based on capture-recapture ratios. It was based entirely on the adults, but was projected to include first-year and second-year young poorly represented in the actual catch. Various errors inherent in the method and the material prevented a highly accurate census, but trends of the figures indicated constant change in population on the Reservation with a minimum of less than three per acre at the time of the annual low in the summer of 1963 and a maximum of approximately 18 per acre at the time of the annual population peak in early autumn of 1961. The population made steady increase through 1958, 1959 and 1960 reaching a high point in 1961, then declined in 1962 and reached its lowest point in 1963.

LITERATURE CITED

Anderson, P.
1942. Amphibians and reptiles of Jackson County, Missouri. Bull. Chicago Acad. Sci., 6(11):203-220.

Bailey, R. M.
1949. Temperature toleration of gartersnakes in hibernation. Ecology, 30: 238-242.

Barbour, R. W.
1950. The reptiles of Big Black Mountain, Harlan County, Kentucky. Copeia, 1950:100-107.

Barton, A. J.
1948. Snake litters. Herpetologica, 4:198.

Batts, B. S.
1961. Intertidal fishes as food of the common garter snake. Copeia, 1961(3):350-351.

Blair, W. F.
1960. The rusty lizard. Univ. Texas Press, Austin, xvi + 185 pp.

Blanchard, F. N. and Blanchard, F. C.
1941a. Factors determining the time of birth in the garter snake, *Thamnophis sirtalis sirtalis* (Linnaeus). Papers Michigan Acad. Sci., Arts and Letters, 26:161-176.

1941b. The inheritance of melanism in the garter snake *Thamnophis sirtalis sirtalis* (Linnaeus). Papers Michigan Acad. Sci., Arts and Letters, 26:177-193.

1942. Mating of the garter snake *Thamnophis sirtalis sirtalis* (Linnaeus). Papers Michigan Acad. Sci., Arts and Letters, 27:215-234.

Boyer, D. A.
1941. Observations on the birth of a brood of garter snakes, *Thamnophis sirtalis sirtalis* Linné. Amer. Midland Nat., 26:334-336.

Breckenridge, W. J.
1944. Reptiles and amphibians of Minnesota. Univ. Minnesota Press, 202 pp.

Breder, C. M., Jr. and Breder, R. B.
1923. A list of fishes, amphibians and reptiles collected in Ash County, North Carolina. Zoologica, 4:3-23.

Cagle, F. R.
1942. Herpetological fauna of Jackson and Union counties, Illinois. Amer. Midl. Nat., 28:164-200.

Carpenter, C. C.
1952a. Comparative ecology of the common garter snake (*Thamnophis s. sirtalis)* the ribbon snake *(Thamnophis s. sauritus),* and Butler's garter snake (*Thamnophis butleri*) in mixed populations. Ecol. Monogr., 22 (4):235-258.

1952b. Growth and maturity of three species of *Thamnophis* in Michigan. Copeia, 1952(4):237-243.

1953. A study of hibernacula and hibernating associations of snakes and amphibians in Michigan. Ecology, 34:74-80.

Carr, A. F., Jr.
1940. A contribution to the herpetology of Florida. Univ. Florida Publ. Biol. series 3:iv + 118 pp.

Cieslak, E. S.
1945. Relations between the reproductive cycle and the pituitary gland in the snake *Thamnophis radix.* Physiol. Zool., 18:299-329.

Clark, R. F.
1949. Snakes of the hill parishes of Louisiana. Jour. Tennessee Acad. Sci., 24(4):244-261.

CONANT, R.
1951. The reptiles of Ohio. (Reprinted with revisionary addenda) Amer. Midl. Nat., 20(1):1-284.

CONANT, R. and DOWNS, A., JR.
1940. Miscellaneous notes on the eggs and young of reptiles. Zoologica, 25:33-48.

CURTIS, L.
1949. The snakes of Dallas County, Texas. Field and Laboratory, 17: 5-13.

DITMARS, R. L.
1936. The reptiles of North America. Doubleday Doran, pp. xvi + 476, 135 pls.

DUELLMAN, W. E.
1951. Notes on the amphibians and reptiles of Greene County, Ohio. Ohio Jour. Sci., 51(6):335-341.

ERNST, S. G.
1945. The food of the red-shouldered hawk in New York State. Auk, 62:452-453.

ERRINGTON, P. L. and BRECKENRIDGE, W. J.
1938. Food habits of the Buteo hawks in the north-central United States. Wilson Bull., 50:113-121.

FINNERAN, L. C.
1948. Reptiles at Branford County, Connecticut. Herpetologica, 4:123-126.

FISHER, E. M.
1928. Variation within a brood of Pacific garter snakes. Univ. Calif. Publ. Zool., 30:221-229.

FITCH, H. S.
1941a. The feeding habits of California garter snakes. California Fish and Game, 27(2):1-32.

1941b. Geographic variation in garter snakes of the species *Thamnophis sirtalis* in the Pacific Coast region of North America. Amer. Midl. Nat., 26(3):570-592.

1958. Home ranges, territories and seasonal movements of vertebrates of The Natural History Reservation. Univ. Kansas Publ. Mus. Nat. Hist., 11(3):63-326.

1960. Autecology of the copperhead. Univ. Kansas Publ. Mus. Nat. Hist., 13:85-288.

1963a. Natural history of the black rat snake (*Elaphe o. obsoleta*) in Kansas. Copeia, 1963(4):649-658.

1963b. Natural history of the racer *Coluber constrictor*. Univ. Kansas Publ. Mus. Nat. Hist., 15:351-468.

FITCH, H. S. and MASLIN, T. P.
1961. Occurrence of the garter snake, *Thamnophis sirtalis*, in the Great Plains and Rocky Mountains. Univ. Kansas Publ. Mus. Nat. Hist., 13:289-308.

FOX, W.
1948. Effect of temperature on development of scutellation in the garter snake, *Thamnophis elegans atratus*. Copeia, 1948(4):252-262.

1951. Relationships among the garter snakes of the *Thamnophis elegans* Rassenkreis. Univ. California Publ. Zool., 50(5):485-530.

1954. Genetic and environmental variation in the timing of reproductive cycles of male garter snakes. Jour. Morph., 95:415-450.

1955. Mating aggregations of garter snakes. Herpetologica, 11(3):176.

FUNKHOUSER, W. D.
1945. Kentucky snakes. Univ. Kentucky Extens., 30 pp.

Gardner, J. B.
1955. A ball of gartersnakes. Copeia, 1955(4):310.
1957. A garter snake "ball." Copeia, 1957(1):48.

Gehlbach, F. R. and Collette, B. B.
1959. Distributional and biological notes on the Nebraska herpetofauna. Herpetologica, 15(3):141-143.

Gloyd, H. K.
1928. The amphibians and reptiles of Franklin County, Kansas. Trans. Kansas Acad. Sci., 31:115-141.

Guthrie, J. E.
1932. Snakes versus birds; birds versus snakes. Wilson Bull., 44:88-113.

Hamilton, W. J., Jr.
1951. The food and feeding behavior of the garter snake in New York State. Amer. Midl. Nat., 46:385-390.

Hamilton, W. J., Jr. and Pollack, J. A.
1956. The food of some colubrid snakes from Fort Benning, Georgia. Ecology, 37:519-526.

Harrison, M. B.
1933. The significance of knobbed keels in the garter snake. Copeia, 1933:1-3.

Hay, O. P.
1891. On the breeding habits, eggs and young of certain snakes. Proc. Indiana Acad. Sci., 1891:106-122.

Hayne, D. W.
1949. Two methods for estimating populations from trapping records. Jour. Mammalogy, 30(4):399-411.

Hebard, W. B.
1951. Notes on the life history of the Puget garter snake, *Thamnophis ordinoides*. Herpetologica, 7(4):177-179.

Hudson, G. E.
1942. The amphibians and reptiles of Nebraska. Nebraska Conserv. Bull., No. 24, 146 pp.

Hudson, G. E. and Davis, D.
1941. Facts concerning the snakes of Nebraska. Lincoln, pp. 1-4.

Klimstra, W. D.
1958. Some observations on snake activities and populations. Ecology, 39:232-239.

Lagler, K. F. and Salyer, J. C., II
1945. Influence of availability on the feeding habits of the common garter snake. Copeia, 1950:100-107.

Langbartel, D. A.
1947. Snakes collected at Camp Eastman, Hancock County, Illinois. Herpetologica, 4(1):27-28.

List, J. E.
1950. Observations on the courtship behavior of Thamnophis sirtalis sirtalis. Herpetologica, 6(3):71-74.

Logier, E. B. S.
1929. Melanism in the garter snake, *Thamnophis sirtalis sirtalis*, in Ontario. Copeia, 172:83-84.
1930. Some additional notes on melanism in *Thamnophis sirtalis sirtalis* in Ontario. Copeia, 1930(1):20.

Logier, E. B. S. and Toner, G. C.
1961. Check list of the amphibians and reptiles of Canada and Alaska. Life Sci. Div. Roy. Ontario Mus., Contr. No. 53, Univ. Toronto Press, 92 pp.

Loomis, R. B.
1956. The chigger mites of Kansas (Acarina, Trombiculidae). Univ. Kansas Sci. Bull., 37, pt. 2(19):1195-1443.

LUETH, F. X.
1941. Effects of temperature on snakes. Copeia, 1941(3):125-132.

MARTOF, B.
1954. Variation in a large litter of garter snakes, *Thamnophis sirtalis sirtalis*. Copeia, 1954(2):100-105.

MATTLIN, R. H.
1948. A large litter of Thamnophis sirtalis sirtalis. Herpetologica, 4(4):149.

MCCAULEY, R. H.
1945. The reptiles of Maryland and the District of Columbia. Published by the author, Hagerstown, Maryland, 194 pp.

MCKEEVER, J. L.
1958. Chipmunk and garter snake. Canadian Field Nat., 72:170.

MEADE, G. P.
1934. Some observations on captive snakes. Copeia, 1934(1):4-5.

MILNES, H.
1946. Amphibians and reptiles at Oxford County, Ontario. Canadian Field Nat., 60:1-4.

MORSE, M.
1904. Batrachians and reptiles of Ohio. Proc. Ohio State Acad. Sci., 4, pt. 3, special paper No. 9:93-144.

MUESEBECK, C. F. W. and KROMBEIN, K. V.
1952. Life zone map. Syst. Zool., 1(1):24-25.

NOBLE, G. K.
1937. The sense organs involved in the courtship of *Storeria*, *Thamnophis* and other snakes. Bull. Amer. Mus. Nat. Hist., 73:673-725.

ORTENBURGER, A. I.
1928. The whip snakes and racers, genera Masticophis and Coluber. Mem. Univ. Michigan Mus., vol. 1, pp. xviii + 247.

PATCH, C. L.
1919. A rattlesnake, melano garter snakes and other reptiles from Point Pelee, Ontario. Canadian Field Nat., 33:60-61.

PUTNAM, F. W.
1869. Do snakes swallow their young? Amer. Nat., 2:34.

RANDALL, P. E.
1940. Seasonal food habits of the marsh hawk in Pennsylvania. Wilson Bull., 52(3):165-172.

REDDICK, G.
1896. Snakes of Turkey Lake. Proc. Indiana Acad. Sci., 1895:261-262.

ROTHMAN, B. and ROTHMAN, N.
1960. First record of a brood of the red-spotted garter snake. Herpetologica, 16(2):100-102.

RUTHVEN, A. G.
1908. Variations and genetic relationships of the garter-snakes. Bull. U. S. Nat. Mus., no. 61, xii + 201 pp.

SCHENCK, J.
1883. A prolific garter snake. Amer. Nat., 16:1008.

SEIBERT, H. C.
1951. Population density of snakes on Penikese Island, Massachusetts. Copeia, 1951:314.

SEIBERT, H. C. and HAGEN, C. W.
1947. Studies on a population of snakes in Illinois. Copeia, 1947(1): 6-22.

SEISS, C. F.
1890. The garter snake. Sci. Amer., 63:105.

SMITH, H. M.
1956. Handbook of amphibians and reptiles of Kansas. Univ. Kansas Mus. Nat. Hist. Misc. Publ., 9:357 pp., 232 figs.

Smith, P. W.
1961. The amphibians and reptiles of Illinois. Bull. Illinois Nat. Hist. Surv., 28(1):1-298.

Stebbins, R. C.
1954. Amphibians and Reptiles of western North America. McGraw-Hill, New York, xxii + 528 pp.

Stewart, P. L.
1960. Lung flukes of snakes, genera *Thamnophis* and *Coluber*, in Kansas. Univ. Kansas Sci. Bull., 41:877-890.

Storer, D. H.
1839. Reports on the ichthyology and herpetology of Massachusetts. Comm. Zool. and Bot. Surv. Mass., Boston, 201-258.

Surface, H. A.
1906. The serpents of Pennsylvania. Pennsylvania State Dept. Agr. Monthly Bull. Div. Zool., 4 (4 and 5):113-208.

Taylor, W. E.
1892. Ophidia of Nebraska. Ann. Rept. Nebraska State Board Agric.:310-357.

Triplehorn, C. A.
1955. Notes on the young of some North American reptiles. Copeia, 1955(3):248-249.

Uhler, F. M., Cottam, C. and Clarke, T. E.
1939. Food of snakes of the George Washington National Forest, Virginia. Trans. 4th Amer. Wildlife Conf., Amer. Wildlife Inst., Washington D. C., 1939:605-632.

Wallace, G. J.
1938. A garter snake with a litter of 73 young. Copeia, 1938(4):203.

Warburton, F.
1950. Notes on the vertebrates of the Sault Ste. Marie region of Ontario. Canadian Field Nat., 64:192-200.

Welter, W. A. and Carr, K.
1939. Amphibians and reptiles of northeastern Kentucky. Copeia, 1939 (3):128-130.

Werler, J. E.
1951. Miscellaneous notes on the eggs and young of Texas and Mexican reptiles. Zoologica, 36(1):37-48.

Werner, W. E., Jr.
1959. Amphibians and reptiles of the Thousand Islands region, New York. Copeia, 1959(2):170-172.

Wood, J. T.
1945. Variation in lengths of newly born garter snakes. Copeia, 1945: 118.

Wright, A. H. and Bishop, S. C.
1915. A biological reconnaissance of the Okefinokee Swamp in Georgia. II. Snakes. Proc. Acad. Nat. Sci. Philadelphia, 67:139-192.

Wright, A. H. and Wright, A. A.
1957. Handbook of snakes of the United States and Canada. Comstock Publ. Associates, Cornell Univ. Press, Vol. 2, pp. i-ix and 565-1106.

Zehr, D. R.
1962. Stages in the normal development of the common garter snake, *Thamnophis sirtalis sirtalis*. Copeia, 1962(2):322-329.

Zorichak, J. L.
1953. The ruffed grouse as a snake eater. Flicker, 25(1):2-3.

Transmitted May 22, 1964.

(Continued from inside of front cover)

9. Variation in the muscles and nerves of the leg in two genera of grouse (Tympanuchus and Pediocecetes). By E. Bruce Holmes. Pp. 363-474, 20 figures. October 25, 1962.
10. A new genus of Pennsylvanian Fish (Crossopterygii, Coelacanthiformes) from Kansas. By Joan Echols. Pp. 475-501, 7 figures. October 25, 1963.
11. Observations on the Mississippi Kite in southwestern Kansas. By Henry S. Fitch. Pp. 503-519. October 25, 1963.
12. Jaw musculature of the Mourning and White-winged doves. By Robert L. Merz. Pp. 521-551, 22 figures. October 25, 1963.
13. Thoracic and coracoid arteries in two families of birds, Columbidae and Hirundinidae. By Marion Anne Jenkinson. Pp. 553-573, 7 figures. March 2, 1964.
14. The breeding birds of Kansas. By Richard F. Johnson. Pp. 575-655, 10 figures. May 18, 1964.
15. The adductor muscles of the jaw in some primitive reptiles. By Richard C. Fox. Pp. 657-680, 11 figures in text. May 18, 1964.

Index. Pp. 681-694.

Vol. 13. 1. Five natural hybrid combinations in minnows (Cyprinidae). By Frank B. Cross and W. L. Minckley. Pp. 1-18. June 1, 1960.
2. A distributional study of the amphibians of the Isthmus of Tehauntepec, México. By William E. Duellman. Pp. 19-72, plates 1-8, 3 figures in text. August 16, 1960.
3. A new subspecies of the slider turtle (Pseudemys scripta) from Coahuila, México. By John M. Legler. Pp. 73-84, plates 9-12, 3 figures in text. August 16, 1960.
4. Autecology of the copperhead. By Henry S. Fitch. Pp. 85-288, plates 13-20, 26 figurs in text. November 30, 1960.
5. Occurrence of the garter snake, Thamnophis sirtalis, in the Great Plains and Rocky Mountains. By Henry S. Fitch and T. Paul Maslin. Pp. 289-308, 4 figures in text. February 10, 1961.
6. Fishes of the Wakarusa river in Kansas. By James E. Deacon and Artie L. Metcalf. Pp. 309-322, 1 figure in text. February 10, 1961.
7. Geographic variation in the North American cyprinid fish, Hybopsis gracilis. By Leonard J. Olund and Frank B. Cross. Pp. 323-348, plates 21-24, 2 figures in text. February 10, 1961.
8. Descriptions of two species of frogs, genus Ptychohyla; studies of American hylid frogs, V. By William E. Duellman. Pp. 349-357, plate 25, 2 figures in text. April 27, 1961.
9. Fish populations, following a drought, in the Neosho and Marais des Cygnes rivers of Kansas. By James Everett Deacon. Pp. 359-427, plates 26-30, 3 figures. August 11, 1961.
10. Recent soft-shelled turtles of North America (family Trionychidae). By Robert G. Webb. Pp. 429-611, plates 31-54, 24 figures in text. February 16, 1962.

Index. Pp. 613-624.

Vol. 14. 1. Neotropical bats from western México. By Sydney Anderson. Pp. 1-8. October 24, 1960.
2. Geographic variation in the harvest mouse. Reithrodontomys megalotis, on the central Great Plains and in adjacent regions. By J. Knox Jones, Jr., and B. Mursaloglu. Pp. 9-27, 1 figure in text. July 24, 1961.
3. Mammals of Mesa Verde National Park, Colorado. By Sydney Anderson. Pp. 29-67, plates 1 and 2, 3 figures in text. July 24, 1961.
4. A new subspecies of the black myotis (bat) from eastern Mexico. By E. Raymond Hall and Ticul Alvarez. Pp. 69-72, 1 figure in text. December 29, 1961.
5. North American yellow bats, "Dasypterus," and a list of the named kinds of the genus Lasiurus Gray. By E. Raymond Hall and J. Knox Jones, Jr. Pp. 73-98, 4 figures in text. December 29, 1961.
6. Natural history of the brush mouse (Peromyscus boylii) in Kansas with description of a new subspecies. By Charles A. Long. Pp. 99-111, 1 figure in text. December 29, 1961.
7. Taxonomic status of some mice of the Peromyscus boylii group in eastern Mexico, with description of a new subspecies. By Ticul Alvarez. Pp. 113-120, 1 figure in text. December 29, 1961.
8. A new subspecies of ground squirrel (Spermophilus spilosoma) from Tamaulipas, Mexico. By Ticul Alvarez. Pp. 121-124. March 7, 1962.
9. Taxonomic status of the free-tailed bat, Tadarida yucatanica Miller. By J. Knox Jones, Jr., and Ticul Alvarez. Pp. 125-133, 1 figure in text. March 7, 1962.
10. A new doglike carnivore, genus Cynaretus, from the Clarendonian Pliocene, of Texas. By E. Raymond Hall and Walter W. Dalquest. Pp. 135-138, 2 figures in text. April 30, 1962.
11. A new subspecies of wood rat (Neotoma) from northeastern Mexico. By Ticul Alvarez. Pp. 139-143, April 30, 1962.
12. Noteworthy mammals from Sinaloa, Mexico. By J. Knox Jones, Jr., Ticul Alvarez, and M. Raymond Lee. Pp. 145-159, 1 figure in text. May 18, 1962.

(Continued on outside of back cover)

(Continued from inside of back cover)

13. A new bat (Myotis) from Mexico. By E. Raymond Hall. Pp. 161-164, 1 figure in text. May 21, 1962.
14. The mammals of Veracruz. By E. Raymond Hall and Walter W. Dalquest. Pp. 165-362, 2 figures. May 20, 1963.
15. The recent mammals of Tamaulipas, México. By Ticul Alvarez. Pp. 363-473, 5 figures in text. May 20, 1963.
16. A new subspecies of the fruit-eating bat, Sturnira ludovici, from western Mexico. By J. Knox Jones, Jr., and Gary L. Phillips. Pp. 475-481, March 2, 1964.
17. Records of the fossil mammal Sinclairella, Family Apatemyidae, from the Chadronian and Orellan. By William C. Clemens. Pp. 483-491. March 2, 1964.

More numbers will appear in volume 14.

Vol. 15. 1. The amphibians and reptiles of Michoacán, México. By William E. Duellman. Pp. 1-148, plates 1-6, 11 figures in text. December 20, 1961.
2. Some reptiles and amphibians from Korea. By Robert G. Webb, J. Knox Jones, Jr., and George W. Byers. Pp. 149-173. January 31, 1962.
3. A new species of frog (Genus Tomodactylus) from western México. By Robert G. Webb. Pp. 175-181, 1 figure in text. March 7, 1962.
4. Type specimens of amphibians and reptiles in the Museum of Natural History, the University of Kansas. By William E. Duellman and Barbara Berg. Pp. 183-204. October 26, 1962.
5. Amphibians and Reptiles of the Rainforests of Southern El Petén, Guatemala. By William E. Duellman. Pp. 205-249, plates 7-10, 6 figures in text. October 4, 1963.
6. A revision of snakes of the genus Conophis (Family Colubridae, from Middle America). By John Wellman. Pp. 251-295, 9 figures in text. October 4, 1963.
7. A review of the Middle American tree frogs of the genus Ptychohyla. By William E. Duellman. Pp. 297-349, plates 11-18, 7 figures in text. October 18, 1963.
8. Natural history of the racer Coluber constrictor. By Henry S. Fitch. Pp. 351-468, plates 19-22, 20 figures in text. December 30, 1963.
9. A review of the frogs of the Hyla bistincta group. By William E. Duellman. Pp. 469-491, 4 figures in text. March 2, 1964.
10. An ecological study of the garter snake, Thamnophis sirtalis. By Henry S. Fitch. Pp. 493-564, plates 23-25, 14 figures in text. May 17, 1965.

More numbers will appear in volume 15.

Vol. 16. 1. Distribution and taxonomy of Mammals of Nebraska. By J. Knox Jones, Jr. Pp. 1-356, pls. 1-4, 82 figures in text. October 1, 1964.

More numbers will appear in volume 16.

- NA - L [Lawrence]

MUS. COM... LIBRARY
DEC 31 19
HARVARD UNIVERSITY

University of Kansas Publications
Museum of Natural History

Volume 15, No. 11, pp. 565-575, 3 figs.

May 17, 1965

Breeding Cycle in the Ground Skink, Lygosoma laterale

BY

HENRY S. FITCH AND HARRY W. GREENE

University of Kansas
Lawrence
1965

University of Kansas Publications, Museum of Natural History
Editors: E. Raymond Hall, Chairman, Henry S. Fitch,
Theodore H. Eaton, Jr.

Volume 15, No. 11, pp. 565-575, 3 figures in text
Published May 17, 1965

University of Kansas
Lawrence, Kansas

PRINTED BY
HARRY (BUD) TIMBERLAKE, STATE PRINTER
TOPEKA, KANSAS
1965

30-3963

S - NA - Lawrence

MUS. COM... OC
LIBRARY
DEC 31 19

Breeding Cycle in the Ground Skink, Lygosoma laterale

BY

HENRY S. FITCH and HARRY W. GREENE

HARVARD
UNIVERSITY

The biology of the ground skink has been made fairly well known through the efforts of many workers, and especially the studies of Lewis (1951) and Johnson (1953). These latter studies were made at Houston, Texas, and New Orleans, Louisiana, respectively, both localities near the Gulf Coast in the southern part of the species' range. Certain important questions were raised but not definitely answered by these studies. Our study was therefore undertaken with the hope of attaining a better knowledge of the breeding cycle of this small skink. We were especially interested in the reproductive potential, specifically, in the time required to attain breeding maturity, the effect of size of female on the number of eggs in her clutch, geographic variation in size of clutch, and the seasonal timing of breeding. Because of the great abundance and extensive geographic range of the ground skink, it was considered an almost ideal subject for such investigation.

In our joint project a total of 523 specimens in The University of Kansas Natural History Museum, the Fort Worth Children's Museum, the Stephen F. Austin State Teachers College collection, and the private collection of Harry W. Greene were examined, from Kansas, Oklahoma, Texas, Missouri, Arkansas, Louisiana, Mississippi, and Georgia. These included several substantial series, notably 22 from near Lewisville, Lafayette County, Arkansas, August 16 and 20, 1926, 31 from Texas, June 22, 27 and 28, 1930, 44 from Huntsville, Walker County, Texas, April 2 and 3, 1963, and 91 from Wister Dam, Le Flore County, Oklahoma, August 11 to 15, 1963.

Reproductive cycles differ in details in different genera and species of reptiles. In the continental United States the prevailing pattern is that of a spring (and/or fall) breeding season, and ovulation in early summer, with the hatchlings or newborn young appearing in late summer or early autumn. One clutch or litter per year has been found to be the most general rule. However, in recent years many species of common lizards, especially iguanids occurring in the southern half of the country, have been found to deviate from this pattern in producing two or more clutches in a single season, for example *Holbrookia texana* (Cagle, 1950:230), *Anolis carolinensis* (Hamlett, 1952:184), *Sceloporus undulatus* (Crenshaw, 1955:273), *Crotaphytus collaris* (Fitch, 1956: 237), *Cnemidophorus* sp. (Milstead, 1957:439; Fitch, 1958:36), *Sceloporus olivaceus* (Blair, 1960:89), *Uta stansburiana* (Tinkle, 1961:230), and *Gerrhonotus liocephalus* (Burkett, 1962:211).

In his study of *Lygosoma,* Johnson (*op. cit.*) found that some adult females

contained simultaneously both oviducal eggs and enlarging follicles (two millimeters or more in diameter) and he suggested the possibility that such individuals might produce two clutches per season. This idea was further supported by Johnson's finding of females containing oviducal eggs in every month from March through August.

There is no true hibernation in this species in the southern part of its range. Lewis (*op. cit.*:234) wrote that at Houston even in mid-winter on warm sunny afternoons the skinks could be found active in the open. Although intermittent periods of inactivity are enforced by the arrival of winter storms and cold fronts, the populations along the Gulf Coast have a relatively long growing season. In winter both Lewis and Johnson found their samples to consist almost entirely of adult skinks, with a few well grown young. Since Johnson found two sizes of young in summer, he was uncertain whether young attained adult size in the first year or in the second year.

In a series of 72 skinks that we examined from Texas, collected in late March and April (mostly from Huntsville, April 2 and 3) only three were below minimum adult size and these were well grown (34, 31 and 29 millimeters snout-vent). These undersized individuals may be interpreted as young that hatched unusually late in the season or that failed to grow at the usual rate. The young present in summer have hatched at different times, and hence do not constitute a clear cut size group, especially since growth is remarkably rapid in the early weeks of life. Also, a series of 64 skinks collected in Texas in June are all adults.

A series collected in Lafayette County, southwestern Arkansas, August 20, 1926, and another series collected by the senior author at Wister Dam, Le Flore County, southeastern Oklahoma, August 11 to 15, 1963, are combined because they represent approximately the same latitudes and times of year. The combined series numbers 113 skinks. Thirty-nine per cent are young of the year and make up a size group fairly distinct from the adults but covering a wide size range—from hatchlings to adolescents (Fig. 2). Since egg-laying was not quite completed at the time of collection, it is evident that many young of the year, perhaps the majority of the second brood, were still not hatched, whereas the oldest young, having hatched in late June, as forerunners of the first brood, had grown for six or more weeks and were already approaching the size of the smallest adults. The young of this combined series show some tendency to bimodality, but the tendency is slight, and perhaps most of these young or all of them represent the hatch of the first brood.

The rate of growth and maturation in the developing ova cannot be definitely determined from the available records, but can be inferred from the information available for other kinds of lizards. In the collared lizard (*Crotaphytus collaris*) a female living under natural conditions was recorded to have laid two successive clutches with an interval of three weeks or a little more (Fitch, 1956:237). Blair (1960:89) found that an interval of about a month between clutches was usual in the rusty lizard (*Sceloporus olivaceus*). Johnson (1960:298) found that in north-central Texas the greater earless lizard (*Holbrookia texana*) produced on the average five clutches of eggs in the course of the breeding season, with an average interval of about 35 days between clutches.

When the Huntsville series of *Lygosoma* was collected, several adults including three females of typical appearance, were kept alive to determine when they would produce eggs. Doubtless their normal cycles were disturbed

by the conditions of captivity. One produced a clutch in late April and another laid on May 31. Other clutches may have been laid and eaten before they were discovered as all the lizards were kept in the same container. When the eggs deposited on May 31 were discovered on the following day, a skink was eating one of them. On August 5 all three females were killed and examined and their ovaries were found to be small. Available evidence suggests that the eggs enlarge rapidly after the breeding season has begun.

Of Kansas females two collected on April 1, 1930, had oviducal eggs and a third had ovarian eggs four millimeters in diameter, although these lizards must have emerged from hibernation only a short time before. In normal years in northeastern Kansas these skinks first appear near the end of March. In 1930 mean temperature for March deviated only .1 degree Fahrenheit from the sixty-year average (Flora, 1948:181).

Of the 71 adult females of *Lygosoma* examined and collected in May, June, and July, 42 had oviducal eggs, 16 had enlarged ovarian eggs, and 13 had small ovaries, suggesting that the period of rapid growth of the eggs in the ovaries is shorter than their period of retention in the oviducts. Johnson (1953:22) reported embryos 1.54 to 3.10 millimeters in length in oviducal eggs, indicating that the early stages of embryonic development are passed in the oviducts before the eggs are laid, and some other species of *Lygosoma* are viviparous. In *L. laterale* oviducal eggs have been reported as early as March 25 in Mississippi (Cook, 1943:19) and April 7 and April 10 in Texas (Lewis, *op. cit.*: 235). Werler (1951:39) recorded clutches laid at San Antonio on April 19, April 27, and May 1. Recorded incubation periods are somewhat variable but most of those recorded approximate one month. Therefore early broods of young might be expected to appear in late May in the vicinity of the Gulf Coast. Johnson (*op. cit.*:18) found no hatchlings before June, but his May sample was relatively small (15). Lewis (*op. cit.*:237) wrote that at Houston in 1947 hatchlings were first noted on June 30. Johnson found that females having oviducal eggs often also had several ovarian eggs considerably enlarged, evidently destined to form a second clutch, with their development already well underway.

All things considered, there must be an interval of somewhat more than a month, perhaps five weeks, between successive clutches in the breeding season. In the region of the Gulf Coast such an interval would allow ample time for four broods that might be spaced about as follows: late April, end of May, beginning of July, first half of August. Because most females have enlarged ova in either ovaries or oviducts or both in this entire period, it seems unlikely that fewer than three clutches would be produced by most individuals.

Farther north the breeding season becomes progressively shorter. Of 19 females collected in Kansas in April, five had oviducal eggs, five had ovarian eggs two to four millimeters in diameter, and the remaining nine had small ovaries. Of six collected in May two had oviducal eggs, two had enlarging ovarian eggs and the remaining two had small ovaries. Two females collected on July 17 and July 19 and three collected on August 17 all had small ovaries. On July 9 at The University of Kansas Natural History Reservation a clutch of three eggs of *Lygosoma* was found associated with a communal nest of the five-lined skink (Fitch, 1954:70). The eggs of the ground skink were within a few days of hatching and therefore must have been laid not later than mid-June. On the Reservation a gravid female was recorded on May 29, 1958. Two other females collected in Douglas County, Kansas, on May 30, 1960,

were both gravid but in one of them the ova were only 3.5 millimeters in diameter, hence probably several weeks short of laying. On the Reservation a hatchling was seen on July 29, 1957, and a juvenile of 29 millimeters was caught on August 20. Of adult females collected in southern Missouri, six taken in the latter half of April all had ovarian follicles 2.5 to 4.5 millimeters in diameter, and others with oviducal eggs were collected on May 3, June 19, and June 26 (3). Of 16 ground skinks collected in southern Missouri in late March and April, six were immature, having the following snout-vent lengths: 27, 30, 32, 34, 34, 37. Smith (1961:169) stated that in southern Illinois eggs are laid in July and hatchlings are abundant in late August. These scanty records indicate that even in the northern part of the range egg-laying probably extends from some time in April into July—allowing ample time for at least two broods. The relatively long and severe winter in the northern part of the range has the effect of compressing the breeding season by preventing breeding in early spring and preventing it in late summer and early autumn, thus enforcing on the population a more uniform breeding schedule than prevails in the southern part of the range.

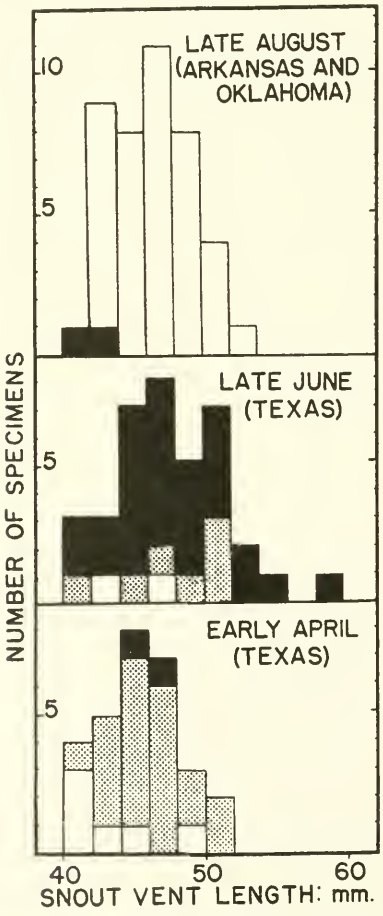


FIG. 1. Histograms showing size and breeding status of adult female ground skinks in three collections. Open columns represent specimens in which ova are small (all less than two millimeters in diameter)—non-breeders or those in an early stage of the breeding cycle; stippled columns represent specimens having enlarged ovarian follicles (two to six millimeters in diameter); black columns represent specimens having oviducal eggs. In early April (lowest figure) most females are in an early stage of the breeding cycle, with ovarian eggs still not mature. Ten weeks later most females are in a late stage of the breeding cycle, with eggs, presumably their second clutches for the season, nearly ready to be laid. By late August, in Arkansas and Oklahoma, the breeding season is over except for a few of the smallest and youngest females, which lag behind the majority in their breeding schedules.

In the series of skinks from Huntsville, Texas, representing early spring, the 28 adult females fall into three distinct groups as regards their reproductive status. Two of near average size (44 and 45 millimeters snout-vent) have oviducal eggs that seem almost ready to be laid. Twenty-one others have smaller, ovarian eggs. Those eggs obviously represent clutches that would have

matured and would have been laid somewhat later in the season. In this group the ova tend to fall in a fairly narrow size range; in 19 skinks they are from three to five millimeters in diameter. In two others eggs are two and one-half and two millimeters in diameter. In the third group, with six females, ovaries are still small, and three of these females are the smallest of the entire series; hence their retardation can probably be attributed to immaturity.

Of the 37 adult female skinks from Texas collected in late June 35 (94.5 per cent) were gravid. Of these 35, 28 had oviducal eggs and probably were near the time of egg-laying, and the remaining individuals had ova 5, 5, 5, 3, 2½, 2½ and 2 millimeters in diameter. First clutches probably had already been laid, and some individuals, notably the two with small ovaries, may have already laid their second clutches. Oviducal eggs in late June probably represented clutches that would have been deposited in early July. Development of the later clutches may be more rapid than development of first clutches, because of the higher temperatures prevailing in summer.

Of six adult females collected in Arkansas in July (no definite dates recorded) four had oviducal eggs and the other two were not breeding. In a female from Texas obtained on July 16 and in three collected on August 17, there were neither enlarging ova nor oviducal eggs, but two others collected on July 20 and August 7, both had oviducal eggs. In the Arkansas-Oklahoma series, representing dates from August 11 to August 20, only the two smallest (40 and 42 millimeters snout-vent) of the 42 adult females had oviducal eggs representing late clutches, and none had enlarging ovarian eggs, indicating that at these localities the breeding season was ending by mid-August.

In the ground skink three is the most frequent number of eggs produced at one laying, but recorded clutches vary from one to seven. Johnson (*op. cit.*:19) found an average of 3.3 ± .05 oviducal eggs in 31 females from Louisiana. Ten additional females from Louisiana examined in our study contained an average of 2.9 eggs. We examined 57 females from Texas that were gravid (having either oviducal eggs or enlarged ovarian follicles) and these had an average clutch of 3.02 ± .15. Lewis (*op. cit.*:235) found an average of 2.82 eggs in 11 females from the vicinity of Houston. But, in 17 females from Arkansas and Oklahoma the average was only 2.35 ± .20. In 17 females from Kansas and 14 from Missouri the clutch averaged 3.77 ± .24. Although smaller than might be desired, this northern series seemed to have a significantly larger number of eggs per clutch than any from the more southern populations.

Johnson (*op. cit.*:19) concluded that a significant correlation between

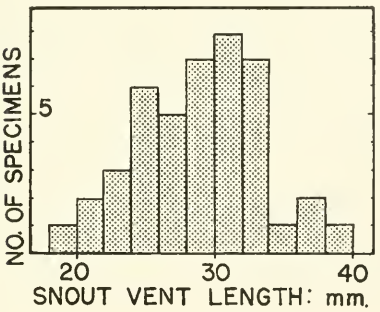


FIG. 2. Lengths of immature ground skinks in a collection from Arkansas and Oklahoma in late August. Those of sizes up to 36 millimeters are almost certainly young of the year hatched early in the summer. At the time of collection some eggs were still to be laid, and doubtless many others laid in late July or early August had not yet hatched. Hence young of the second brood probably are poorly represented or not represented at all in this sample.

number of eggs per clutch and snout-vent length of female did not exist in the series that he examined, as the regression coefficient was .069. However, the trend of his data did suggest a correlation, with the two-egg clutches found mostly in the smaller females, and the four- or five-egg clutches found in the larger females. In our study we found a definite positive correlation between size of female and number of eggs in clutch, as follows:

11 females 54 to 59 millimeters averaged 3.63 ± .41 eggs
45 females 48 to 53 millimeters averaged 3.76 ± .16 eggs
61 females 42 to 47 millimeters averaged 2.65 ± .11 eggs
13 females 36 to 41 millimeters averaged 1.84 ± .18 eggs

Or, arranging the same data differently, grouped according to the number of eggs in the clutch:

10 females with 1-egg clutches averaged 43.3 ± 1.31 millimeters
36 females with 2-egg clutches averaged 44.6 ± .57 millimeters
43 females with 3-egg clutches averaged 47.0 ± .62 millimeters
26 females with 4-egg clutches averaged 49.4 ± .59 millimeters
11 females with 5-egg clutches averaged 50.5 ± 1.78 millimeters
3 females with 6-egg clutches averaged 52.6 millimeters
1 female with 7-egg clutch was 52 millimeters

The correlation between number of eggs in clutch and snout-vent length of female is further clarified by Fig. 3. It would perhaps be correct to say that the smallest adult females always have minimal numbers of eggs per clutch, and that with increasing average size proportionately larger clutches are

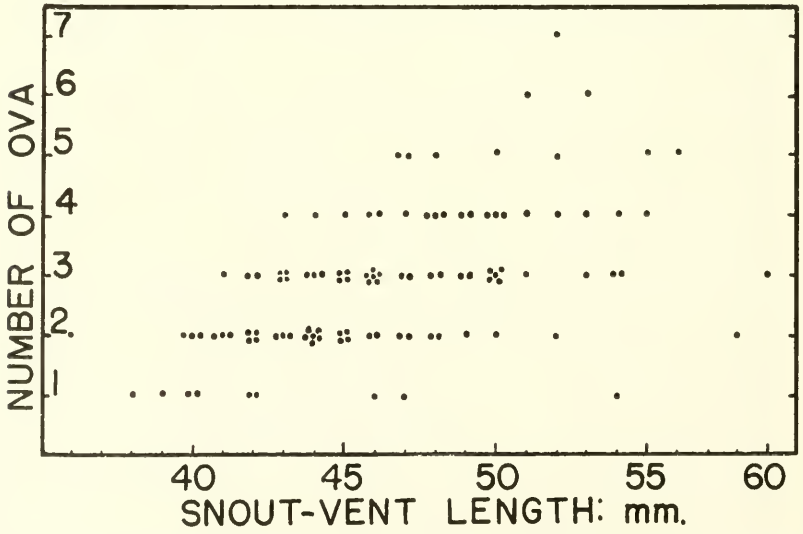


FIG. 3. Number of ova and size in fecund ground skinks. On the average, the larger females produce more eggs, but occasionally large females produce small clutches.

produced, but large females occasionally produce clutches with a small number of eggs perhaps because of senility, lateness of season or for other reasons.

The lack of opportunity for individuals to produce successive clutches in one season in the northern part of the range because of the relatively short

breeding season is in part compensated for by a greater number of eggs per clutch. Larger size in northern populations may be a factor also. Over the extensive geographic range of *Lygosoma laterale* no subspecies have been named and geographic variation has not been demonstrated. In our study we found that ground skinks from Kansas differed slightly in general appearance from those of the Gulf Coast, and averaged slightly larger but the difference is not necessarily indicative of significant geographic variation. Table 1 shows the average sizes of adult males and females (those 36 millimeters or more in snout-vent length) in the larger series examined by us. It is shown that females are approximately four millimeters longer than their male counterparts. Differences in age structures of the population samples involved are probably more important than geographic variation in affecting the figures. This is illustrated by the two series from Texas. Almost all of the skinks collected in early April were adults, but many of them were recently matured individuals of the previous years' brood. The June sample represents essentially the same population after approximately ten weeks of additional growth; both sexes had made substantial gains, but the females had grown more than the males.

TABLE 1.—SNOUT-VENT LENGTHS IN MILLIMETERS OF MALE AND FEMALE GROUND SKINKS IN SEVERAL SERIES

Locality	Females	Males
Kansas	48.9 ± .81 in 37	43.0 ± .84 in 21
Oklahoma	46.3 ± .47 in 37	42.3 ± .53 in 27
Arkansas	46.4 ± .74 in 27	42.1 ± .69 in 22
Louisiana (Johnson, 1953:23; females with oviducal eggs only)	47.3 ± .88 in 32	.....
Texas (in April)	45.3 ± 1.24 in 19	42.6 ± .46 in 31
Texas (in June)	47.2 ± .67 in 37	43.2 ± .62 in 27

In keeping with their larger size, the June-taken females from Texas averaged slightly more eggs per clutch—3.0, as compared with 2.76 for the April-taken females. In this southern part of the range June is the peak of the breeding season and the clutches produced that month are often both preceded and followed by others. Late clutches, produced as the breeding season wanes, probably tend to be smaller than others produced earlier. In our Arkansas-Oklahoma sample, eight females collected in April averaged 2.88 enlarged follicles or oviducal eggs, but in six females collected in July and August there was an average of only 1.83. It might be expected that at latitudes where the growing season is shortened to the extent that broods are eliminated, the size of clutch would increase abruptly.

In summary, the ground skinks of the Gulf Coast have a long growing season with hibernation short and intermittent. There is ample time for at least four broods and some individuals possibly produce more. The majority of females have developing ovarian follicles in early April and first clutches

of eggs are laid from late April through May. Some young must hatch before the end of May but none has been recorded until June. A few females are several weeks ahead of the majority in their breeding schedule; others are still not sexually mature in early spring and their breeding schedule is several weeks behind that of the majority. In the northern part of the range at the latitude of Kansas the breeding season is relatively short, but the average female probably produces at least two clutches in the seven-months growing season. At this latitude egg-laying occurs in late April, June and July. At the latitude of southern Oklahoma and Arkansas egg-laying extends into early August.

Three is the modal number of eggs per clutch but in the north clutches with four, five, and even six eggs are common. There is positive correlation between size of female and number of eggs per clutch. Those females that are of minimum adult size or only slightly larger produce clutches with fewer than the average number of eggs. The largest females produce the largest clutches but occasionally some of them produce small clutches. The time of year also affects number of eggs per clutch; toward the end of the breeding season clutches have fewer eggs on the average, even though females average larger then.

Financial assistance from the National Science Foundation (G-16104) is acknowledged. For the loan of specimens from the collections in their care, and for other courtesies extended to us in the course of this study we are indebted to Mr. John R. Preston of the Childrens' Museum, Fort Worth, Texas, and to Dr. William E. Duellman and Mr. Charles J. Cole of The University of Kansas Museum of Natural History.

LITERATURE CITED

Blair, W. F.
1960. The rusty lizard. Univ. Texas Press, Austin, xvi + 185 pp.

Burkett, R. D.
1962. Two clutches of eggs in the lizard, *Gerrhonotus liocephalus infernalis*. Herpetologica, 18(3):211.

Cagle, F. R.
1950. Notes on *Holbrookia texana* in Texas. Copeia, 1950(3):230.

Cook, F. A.
1943. Alligators and lizards of Mississippi. Surv. Bull., Mississippi State Game and Fish Comm., pp. 1-20.

Crenshaw, J. W., Jr.
1955. The life history of the southern spiny lizard, *Sceloporus undulatus undulatus* Latreille. American Midl. Nat., 54(2):257-298.

Fitch, H. S.
1954. Life history and ecology of the five-lined skink, *Eumeces fasciatus*. Univ. Kansas Publs. Mus. Nat. Hist. 8(1):1-156.

1956. An ecological study of the collared lizard (*Crotaphytus collaris*). Univ. Kansas Publs. Mus. Nat. Hist. 8(3):213-274.

1958. Natural history of the six-lined racerunner (*Cnemidophorus sexlineatus*). Univ. Kansas Publs. Mus. Nat. Hist. 11(2):11-62.

Flora, S. D.
1948. Climate of Kansas. Report Kansas State Board Agric., 67, xii + 320 pp.

Hamlett, G. W. D.
1952. Notes on breeding and reproduction in the lizard *Anolis carolinensis*. Copeia, 1952 (3):183-185.

Johnson, C.
1960. Reproductive cycle in females of the greater earless lizard, *Holbrookia texana*. Copeia, 1960(4):299-300.

Johnson, R. M.
1953. A contribution on the life history of the lizard *Scincella laterale* (Say). Tulane Studies in Zoology, 1(2):11-27.

Lewis, T. H.
1951. The biology of *Leiolopisma laterale* (Say). American Midl. Nat., 45:232-240.

Milstead, W. W.
1957. Some aspects of competition in natural populations of whiptail lizards (genus Cnemidophorus). Texas Jour. Sci. 9(4):410-447.

Smith, P. W.
1961. The amphibians and reptiles of Illinois. Bull. Illinois Nat. Hist. Surv., 28(1):1-298.

Tinkle, D. W.
1961. Population structure and reproduction in the lizard, *Uta stansburiana stejnegeri*. American Midl. Nat., 66(1):206-234.

Werler, J. E.
1951. Miscellaneous notes on the eggs and young of Texas and Mexican reptiles. Zoologica, 36(1):37-48.

30-3963

S-NH-L[awrence]

UNIVERSITY OF KANSAS PUBLICATIONS
MUSEUM OF NATURAL HISTORY

Volume 15, No. 12, pp. 577-614, 1 fig.
June 22, 1965

MUS. COM. . . OC
LIBRARY
DEC 3 1 1965
HARVARD
UNIVERSITY

Amphibians and Reptiles From the Yucatan Peninsula, México

BY

WILLIAM E. DUELLMAN

UNIVERSITY OF KANSAS
LAWRENCE
1965

UNIVERSITY OF KANSAS PUBLICATIONS
MUSEUM OF NATURAL HISTORY

Institutional libraries interested in publications exchange may obtain this series by addressing the Exchange Librarian, University of Kansas Library, Lawrence, Kansas. Copies for individuals, persons working in a particular field of study, may be obtained by addressing instead the Museum of Natural History, University of Kansas, Lawrence, Kansas. There is no provision for sale of this series by the University Library, which meets institutional requests, or by the Museum of Natural History, which meets the requests of individuals. Nevertheless, when individuals request copies from the Museum, 25 cents (for each 100 pages or part thereof) should be included for the purpose of defraying the costs of wrapping and mailing. For certain longer papers an additional amount indicated below, is to be included toward the cost of production.

° An asterisk designates those numbers of which the Museum's supply (not necessarily the Library's supply) is exhausted. Materials published to date, in this series, are as follows:

Vol. 1. Nos. 1-26 and index. Pp. 1-638, 1946-1950.

°Vol. 2. (Complete) Mammals of Washington. By Walter W. Dalquest. Pp. 1-444, 140 figures in text. April 9, 1948.

°Vol. 3. Nos. 1-4 and index. Pp 1-681. 1951.

°Vol. 4. (Complete) American weasels. By E. Raymond Hall. Pp. 1-466, 41 plates, 31 figures in text. December 27, 1951.

Vol. 5. Nos. 1-37 and index. Pp. 1-676, 1951-1953.

°Vol. 6. (Complete) Mammals of Utah, *taxonomy and distribution.* By Stephen D. Durrant. Pp. 1-549, 91 figures in text, 30 tables. August 10, 1952.

Vol. 7. Nos. 1-15 and index. Pp. 1-651, 1952-1955.

Vol. 8. Nos. 1-10 and index. Pp. 1-675, 1954-1956.

Vol. 9. Nos. 1-23 and index. Pp. 1-690, 1955-1960.

Vol. 10. 1. Studies of birds killed in nocturnal migration. By Harrison B. Tordoff and Robert M. Mengel. Pp. 1-44, 6 figures in text, 2 tables. September 12, 1956.

2. Comparative breeding behavior of Ammospiza caudacuta and A. maritima. By Glen E. Woolfenden. Pp. 45-75, 6 plates, 1 figure. December 20, 1956.

°3. The forest habitat of the University of Kansas Natural History Reservation. By Henry S. Fitch and Ronald R. McGregor. Pp. 77-127, 2 plates, 7 figures in text, 4 tables. December 31, 1956.

4. Aspects of reproduction and development in the prairie vole (Microtus ochrogaster). By Henry S. Fitch. Pp. 129-161, 8 figures in text, 4 tables. December 19, 1957.

5. Birds found on the Arctic slope of northern Alaska. By James W. Bee. Pp. 163-211, plates 9-10, 1 figure in text. March 12, 1958.

°6. The wood rats of Colorado: distribution and ecology. By Robert B. Finley, Jr. Pp. 213-552, 34 plates, 8 figures in text, 35 tables. November 7, 1958.

7. Home ranges and movements of the eastern cottontail in Kansas. By Donald W. Janes. Pp. 553-572, 4 plates, 3 figures in text. May 4, 1959.

8. Natural history of the salamander, Aneides hardyi. By Richard F. Johnston and Gerhard A. Schad. Pp. 573-585. October 8, 1959.

9. A new subspecies of lizard, Cnemidophorus sacki, from Michoacán, México. By William E. Duellman. Pp. 587-598, 2 figures in text. May 2, 1960.

10. A taxonomic study of the middle American snake, Pituophis deppei. By William E. Duellman. Pp. 599-610, 1 plate, 1 figure in text. May 2, 1960.

Index. Pp. 611-626.

Vol. 11. Nos. 1-10 and index. Pp. 1-703, 1958-1960.

Vol. 12. °1. Functional morphology of three bats: Eumops, Myotis, Macrotus. By Terry A. Vaughan. Pp. 1-153, 4 plates, 24 figures in text. July 8, 1959.

°2. The ancestry of modern Amphibia: a review of the evidence. By Theodore H. Eaton, Jr. Pp. 155-180, 10 figures in text. July 10, 1959.

3. The baculum in microtine rodents. By Sydney Anderson. Pp. 181-216, 49 figures in text. February 19, 1960.

°4. A new order of fishlike Amphibia from the Pennsylvanian of Kansas. By Theodore H. Eaton, Jr., and Peggy Lou Stewart. Pp. 217-240, 12 figures in text. May 2, 1960.

5. Natural history of the bell vireo. By Jon C. Barlow. Pp. 241-296, 6 figures in text. March 7, 1962.

6. Two new pelycosaurs from the lower Permian of Oklahoma. By Richard C. Fox. Pp. 297-307, 6 figures in text. May 21, 1962.

7. Vertebrates from the barrier island of Tamaulipas, México. By Robert K. Selander, Richard F. Johnston, B. J. Wilks, and Gerald G. Raun. Pp. 309-345, plates 5-8. June 18, 1962.

8. Teeth of Edestid sharks. By Theodore H. Eaton, Jr. Pp. 347-362, 10 figures in text. October 1, 1962.

(Continued on inside of back cover)

University of Kansas Publications
Museum of Natural History

Volume 15, No. 12, pp. 577-614, 1 fig.

June 22, 1965

Amphibians and Reptiles From the Yucatan Peninsula, México

BY

WILLIAM E. DUELLMAN

University of Kansas
Lawrence
1965

S-NA-[Lawrence]

University of Kansas Publications, Museum of Natural History

Editors: E. Raymond Hall, Chairman, Henry S. Fitch,
Theodore H. Eaton, Jr.

Volume 15, No. 12, 577-614, 1 fig.
Published June 22, 1965

MUS. COM. . . OOL
LIBRARY
DEC 31 19[illegible]
HARVARD
UNIVERSITY

University of Kansas
Lawrence, Kansas

PRINTED BY
HARRY (BUD) TIMBERLAKE, STATE PRINTER
TOPEKA, KANSAS
1965

30-3966

Amphibians and Reptiles From the Yucatan Peninsula, México

BY

WILLIAM E. DUELLMAN

CONTENTS

PAGE

Introduction ... 579
Acknowledgments ... 582
Summary of Field Work ... 582
Gazetteer ... 583
Annotated List of Species ... 585
Amphibia ... 586
Caudata ... 586
Salientia ... 586
Reptilia ... 590
Testudines ... 590
Crocodilia ... 593
Sauria ... 593
Serpentes ... 605
Summary ... 611
Literature Cited ... 612

INTRODUCTION

The Yucatan Peninsula (Península de Yucatán) is a northeastern projection of Middle America lying between the Gulf of Mexico and the Caribbean Sea. Included in its area of 143,500 square kilometers are the Mexican states of Campeche and Yucatán, and the territory of Quintana Roo, plus large parts of British Honduras and the Department of El Petén in Guatemala. The peninsula has a mean breadth of about 320 kilometers and a coast line of about 1100 kilometers. The coast on the north and west is low, sandy, and semibarren. The eastern coast consists of playas and bluffs, indented with bays and bordered by several islands, the largest being Isla de Cozumel. The peninsula is almost wholly composed of porous limestone, locally coraline, forming a low tableland, which gradually rises to the south. The rock is covered by a thin layer of soil in the north and deeper soils in the south. One of the features of the karst topography in the northern part of the peninsula is the presence of many natural sinks (locally called *cenotes*); similar depressions containing water in the southern part of the peninsula are

called *aguadas*. Except in the extreme southern part of the peninsula, surface streams are absent. The climate is hot with seasonal rainfall, varying from about 450 mm. annually in the northwestern part to more than 2000 mm. annually in the south. A prolonged dry season lasts from November to May. Deeper soils and more rainfall in the southern part of the peninsula provide adequate conditions for the development of a lush evergreen forest, characterized by dense undergrowth beneath trees, some attaining heights of more than 30 meters. The tall evergreen forest in the southern part of the peninsula does not meet the phyto-sociological requirements of true rainforest and is best referred to as quasi-rainforest. Northward in the peninsula the vegetation becomes lower, more xeric, and deciduous. Along the northern coast the trees seldom attain heights of more than eight meters, but tall evergreen forest extends northward into northern Quintana Roo on the eastern edge of the peninsula, where soils are deep. Possibly because of local edaphic conditions, savannas or "islands of grassland" occur in the southwestern part of the peninsula; small clumps of large evergreen treees surround many of the larger cenotes in the northern part of the peninsula, which is dominated by low, deciduous scrub forest.

This extensive and interesting peninsula has received only cursory attention from zoologists, most of whom have been associated with archeological expeditions working at such Mayan ruins as Chichén-Itzá, Tulum, and Uxmal in the state of Yucatán. A notable exception is the extensive survey of the peninsular avifauna undertaken by Paynter (1955).

Gaige (1936) reported on amphibians and reptiles from Yucatán and Campeche and summarized the earlier literature on the herpetology of the peninsula. Schmidt and Andrews (1936) reported on snakes collected by Andrews at Chichén-Itzá in the summer of 1934, and Andrews (1937) reported on additional snakes that he obtained in Yucatán and Quintana Roo in July and August, 1937. Smith (1938) reported on a collection made in southwestern Campeche and in Yucatán by him and H. Devlin Thomas in the summer of 1936. For more than 20 years no collections of amphibians and reptiles were made in the peninsula, except for a small, but significant, collection from Felipe Carrillo Puerto, Quintana Roo, reported by Peters (1953). Maslin (1963) reported on the lizards and frogs obtained in Yucatán and northern Quintana Roo in the summer of 1959 by a field party from the University of Colorado Museum, and McCoy (1963) recorded *Eumeces sumichrasti* from the northeastern part of the peninsula.

In the summer of 1962 the Museum of Natural History at the University of Kansas initiated a field program to survey the vertebrate fauna of the Yucatan Peninsula. The field work continued until early June, 1963. One field party in the summer of 1962 consisted of the author and six students (the summer field course in vertebrate zoology). The other field party, which most of the time worked jointly with the first party, consisted of J. Knox Jones, Jr. and four students, who were specifically working on a survey of Middle American terrestrial vertebrates and their ectoparasites. In the rainy season of 1962 we travelled extensively in the peninsula and obtained large and varied collections of vertebrates. In mid-December, 1962, Percy L. Clifton, field collector for the Museum of Natural History, began work in the peninsula; Clifton spent the dry season of 1962-63 working in areas that had not been studied in the previous rainy season. The field work was designed to cover as

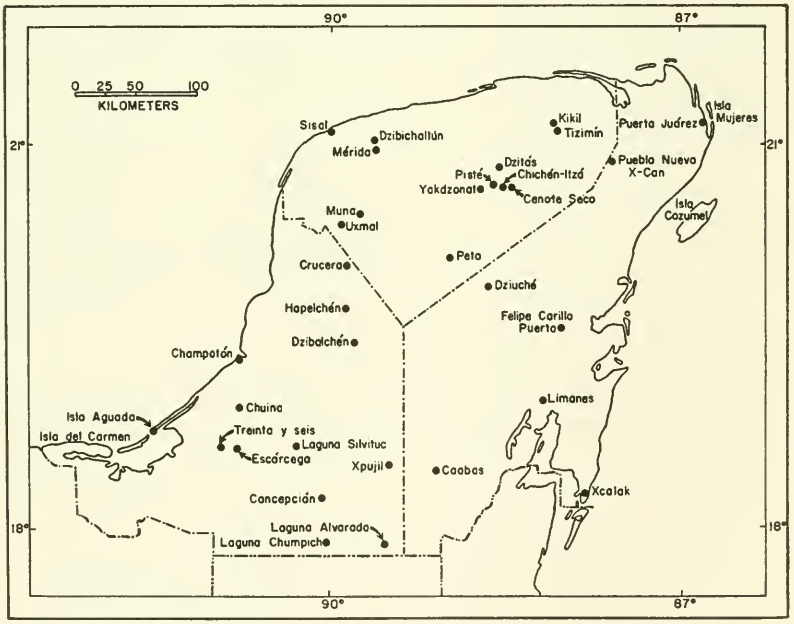


FIG. 1. Map of the Yucatan Peninsula showing localities where specimens were collected.

much of the peninsula as possible and to sample the faunas in the tall evergreen forests in the southern part of the peninsula, as well as the scrub forests and intermediate habitats to the north.

With the exception of a synoptic collection presented to the De-

partamento de la Fauna Silvestre, Dirección General de Caza, México, D. F., all of the specimens obtained are in the collections of the museum of Natural History at the University of Kansas, to which collection catalogue numbers given in the text refer.

The purpose of the present paper is to put on record the specimens of amphibians and reptiles obtained in the Yucatan Peninsula and to comment, as necessary, on taxonomic, distributional, and ecological aspects of the specimens and data. No attempt is made here to analyze the faunistics of the amphibians and reptiles of the peninsula, for an analysis of the herpetofauna of the entire lowland region comprising the Yucatan Peninsula and El Petén, Guatemala, is in preparation by L. C. Stuart and the author.

Acknowledgments

My first debt of gratitude is to the members of the field parties who obtained much of the material (specimens and detailed field notes) reported herein; thus, I thank Ticul Alvarez, A. Binion Amerson, Richard C. Fox, J. Knox Jones, Jr., Erwin E. Klaas, Linda T. Klaas, Thomas E. Lovejoy, III, Jack G. Makepeace, Dwight R. Platt, William C. Stanley, Jerome B. Tulecke, and John Wellman. I am grateful to Percy L. Clifton for his determination in seeking out certain species that I requested him to find. The field parties benefited from arrangements made for us by Eduardo C. Welling of Mérida, and our field work was enhanced by quarters provided at the Campo Experimental Forestal "El Tormento" at Escárcega, Campeche, by Ing. Hector Flores S., at Pueblo Nuevo X-Can, Quintana Roo, by Pablo Alimilla, at Felipe Carrillo Puerto, Quintana Roo, by Fernando Esquival Montoño, and at Pisté, Yucatán, by Luis V. Polanco. For helpful suggestions we also are indebted to Padre Joseph Early of Felipe Carrillo Puerto. Last, but not least, a host of Mayans, young and old alike, helped in innumerable ways, especially as guides and collectors; their enthusiastic efforts greatly enriched our collections.

The summer field course in vertebrate zoology was supported in part by the Museum of Natural History and by a grant from the National Science Foundation (G 20939, Special Projects in Science Education); the field party working on terrestrial vertebrates and their ectoparasites was supported by the United States Army Medical Research and Development Command (Contract No. DA 49 193 MD 2215). Only through the combined resources and support of these institutions was the field work made possible. The late Ing. Luis Macías Arellano of the Departamento de la Fauna Silvestre, Dirección General de Caza, México, D. F., generously provided the necessary permits.

I am grateful to J. Knox Jones, Jr. and Erwin E. Klaas for reading parts of this paper and offering helpful comments, and I am indebted to L. C. Stuart of the University of Michigan for his helpful criticism of the manuscript.

SUMMARY OF FIELD WORK

In the summer of 1962 a combined field party consisting of J. Knox Jones, ten students, and the author made collections of terrestrial vertebrates and their ectoparasites in the Yucatan Peninsula. Our field work centered in southwestern Campeche from July 6 to 18; there we worked out of camps on

Isla del Carmen, at 5 kilometers south of Champotón, and at 7.5 kilometers west of Escárcega. On July 20 we moved to Pisté, Yucatán, and from a base camp there collected at Chichén-Itzá, north to Dzitás, and west to Yokdzonot. From July 27 to 30 we were at Pueblo Nuevo X-Can, Quintana Roo, and on July 31 we moved to a campsite 4 kilometers west-southwest of Puerto Juárez, Quintana Roo. Some of us travelled by boat to Isla Mujeres on August 1 and returned to Puerto Juárez on August 3. The following day the entire field party drove to Mérida, and on August 7 some of us flew to Isla de Cozumel, where we stayed until August 11; other members of the field party spent August 7-11 at Sisal, Yucatán. On August 13 we drove from Mérida to Felipe Carillo Puerto and set up camp 4 kilometers north-northeast of the town. We returned to Mérida on August 17; some of us spent the following day at Sisal. We left Mérida on August 20, collected briefly at Uxmal, and drove to the United States.

Percy L. Clifton arrived in Escárcega, Campeche, on December 16, 1962. From there he worked eastward across the southern part of the peninsula until April 15, 1963. He collected vertebrates at Escárcega, Treinta y seis, Chuina, Laguna Silvituc, Laguna Chumpich, Laguna Alvarado, Concepción, and Xpujil, Campeche, and at Caobas, Xcalak, and Limones, Quintana Roo. From April 16 to May 1 he collected in Yucatán and obtained specimens at Peto, Mérida, Kikil, and Tizimín. After travelling elsewhere in México throughout most of May, Clifton returned to Campeche on May 30 to spend a week at Dzibalchén, three days at Isla Aguada, and two days on Isla del Carmen.

Erwin E. Klaas and Linda T. Klaas arrived in Yucatán on July 25, 1963, and spent a week collecting amphibians and reptiles at Muna, Mérida, and Dzibichaltún.

Gazetteer

The localities where the herpetological specimens reported herein were obtained are listed alphabetically within the states below; each locality is shown on the accompanying map (Fig. 1).

Campeche

Champotón.—Lat. 19° 21′ N, Long. 90° 43′ W, sea level. A town on the Gulf of Mexico. We collected principally in the vicinity of our camp 5 kilometers south of the town in mixed scrub forest and quasi-rainforest.

Chuina.—Lat. 18° 58′ N, Long. 90° 41′ W, Elev. 25 m. A village about 45 kilometers south of Champotón. Savanna and open forest; three large, permanent aguadas.

Concepción.—Lat. 18° 13′ N, Long. 90° 04′ W, Elev. 65 m. A small village in dense quasi-rainforest in southeastern Campeche.

Crucero.—Lat. 20° 01′ N, Long. 89° 45′ W, Elev. 70 m. A small village on the road north of Hopelchén. Dense scrub forest.

Dzibalchén.—Lat. 19° 24′ N, Long. 89° 45′ W, Elev. 100 m. A village in low scrub forest amidst rolling rocky hills.

Escárcega.—Lat. 18° 37′ N, Long. 90° 44′ W, Elev. 65 m. A town in southwestern Campeche. Field work was carried out in the vicinity of an agricultural station, 7.5 kilometers west of the town. Quasi-rainforest.

Hopelchén.—Lat. 19° 45′ N, Long. 89° 51′ W, Elev. 80 m. Village in dense scrub forest. Specimens were obtained 8 kilometers north and 11 kilometers west of the town.

Isla Aguada.—Lat. 18° 48′ N, Long. 91° 31′ W, sea level. A village on a sandy point projecting southwestward from the mainland towards Isla del Carmen. Sandy soil, beach, coconut plantations, and some mangrove swamp.

Isla del Carmen.—Lat. 18° 43′ N, Long. 91° 41′ W, sea level to 2 meters. An island in the mouth of Laguna de Términos. Coconut plantations and mangrove swamp. Most of our specimens came from the vicinity of our camp one kilometer southwest of Puerto Real, which is on the northeastern end of the island.

Laguna Alvarado.—Lat. 17° 51′ N, Long. 89° 33′ W, Elev. 150 m. A lagoon in tall, dense quasi-rainforest, 55 kilometers south of Xpujil and approximately 10 kilometers north of the Guatemalan border.

Laguna Chumpich.—Lat. 19° 24′ N, Long. 90° 03′ W, Elev. 150 m. A lagoon about 1 kilometer in length surrounded by tall quasi-rainforest.

Laguna Silvituc.—Lat. 18° 40′ N, Long. 90° 15′ W, Elev. 60 m. Lake in the midst of quasi-rainforest. Collections were made at the village of Silvituc on the north edge of the lake and at a camp about 10 kilometers east of the lake.

Treinta y seis.—Lat. 18° 48′ N, Long. 91° 31′ W, Elev. 65 m. A small village at the edge of an aquada in quasi-rainforest, 13 kilometers west and one kilometer north of Escárcega.

Xpujil.—Lat. 18° 31′ N, Long. 89° 29′ W, Elev. 250 m. A village on the road from Escárcega to Chetumal; collections were made at the village, at a sawmill 9 kilometers north of the village, and at an aguada 20 kilometers north of the village. Quasi-rainforest.

Quintana Roo

Caobas.—Lat. 18° 27′ N, Long. 89° 06′ W, Elev. 175 m. A small village (Ejido) and lagoon, 3 kilometers south of the Escárcega-Chetumal road at kilometer post 88.

Dziuché.—Lat. 19° 54′ N, Long. 88° 35′ W, Elev. 40 m. A small village in cut-over scrub forest in northwestern Quintana Roo.

Felipe Carrillo Puerto.—Lat. 19° 35′ N, Long. 88° 02′ W, Elev. 30 m. A town in central Quintana Roo. We camped and collected at Rancho San Miguel, 4 kilometers north-northeast of town. Transitional evergreen forest (some trees 25 meters high) with some corozo palms; a deep aguada bordered on the north by an extensive marsh.

Isla Cozumel.—Lat. 20° 27′ N, Long. 86° 26′ W, sea level to 5 meters. A large island, 18 kilometers east of mainland in Caribbean Sea. Our collections were made on the northwestern part of the island from 2 to 5 kilometers north-northeast of the town of San Miguel in low dense scrub forest and coastal strand.

Isla Mujeres.—Lat. 21° 15′ N, Long. 86° 48′ W, sea level to 30 meters. A small, long island in the Caribbean Sea about 4 kilometers off the northeastern end of the peninsula. Our collections were made on the beach at the northern end of the island, in dense scrub forest at Rancho Pirata in the middle of the island, and in low scrub forest and paddle cactus association on a high rocky bluff on the southern end of the island.

Limones.—Lat. 18° 59′ N, Long. 88° 10′ W, Elev. 15 m. A small village north-northwest of the end of Bahía de Chetumal. Collections were made in quasi-rainforest north of the village.

Pueblo Nuevo X-Can.—Lat. 20° 52′ N, Long. 87° 26′ W, Elev. 10 m. A small village 5 kilometers east of X-Can, Yucatán, in tall quasi-rainforest (25 meters) with dense underbrush. We obtained specimens from the immediate vicinity of the town and from caves 1.5 kilometers south and 1 kilometer east, and 1.5 kilometers south and 7 kilometers east of the town.

Puerto Juárez.—Lat. 21° 10′ N, Long. 86° 49′ W, sea level. A small port on the Caribbean Coast with alternating white sand beach and limestone shore, bordered inland by mangroves. We obtained specimens along the beach and from our camp in dense evergreen forest 4 kilometers west-southwest of the village.

Xcalak.—Lat. 18° 16′ N, Long. 87° 49′ W, sea level. A village and ruins on the Caribbean Coast of the peninsula southeast of Chetumal (east of Bahía de Chetumal). Coconut plantations and mangrove swamp.

Yucatán

Cenote Seco.—Lat. 20° 41′ N, Long. 88° 23′ W, Elev. 10 m. A sink-hole 2 kilometers east of Chichén-Itzá. Growing in the sink-hole are many plants characteristic of the wet parts of the peninsula farther south, including elephant ears, mamey, and figs. Low, xeric scrub forest surrounds the cenote.

Chichén-Itzá.—Lat. 20° 41′ N, Long. 88° 25′ W, Elev. 10 m. A small village and extensive Mayan ruins in dense scrub forest. We collected at Cenote Xtolok at the south edge of the village and at small solution pits in the scrub forest 9 and 12 kilometers east of the village.

Dzibichaltún.—Lat. 21° 02′ N, Long. 89° 34′ W, Elev. 5 m. Collections were made in open, low scrub forest just west of the ruins of Dzibichaltún.

Dzitás.—Lat. 20° 50′ N, Long. 88° 26′ W, Elev. 10 m. A village in dense scrub forest 18 kilometers by road north-northeast of Pisté.

Kikil.—Lat. 21° 12′ N, Long. 88° 09′ W, Elev. 8 m. A ranch 6 kilometers north of Tizimín; cultivated fields and scrub forest.

Mérida.—Lat. 20° 58′ N, Long. 89° 35′ W, Elev. 10 m. Capital of the state of Yucatán. Our specimens came from just west of the airport, 6 kilometers south of town in open fields and scrub forest.

Muna.—Lat. 20° 29′ N, Long. 89° 42′ W, Elev. 20 m. Collections were made in dense scrub forest 7 kilometers north of the town.

Peto.—Lat. 20° 07′ N, Long. 88° 57′ W, Elev. 30 m. A town in south-central Yucatán; dense scrub forest and cultivated fields.

Pisté.—Lat. 20° 42′ N, Long. 88° 28′ W, Elev. 10 m. A village in dense scrub forest. We collected north and west of the village. Many specimens were purchased from residents.

Sisal.—Lat. 21° 10′ N, Long. 90° 00′ W, sea level. A small village on the northwestern coast of the peninsula. We collected in the cactus-sea grape association behind the beach at 3 and at 13 kilometers west-southwest of the village.

Tizimín.—Lat. 21° 09′ N, Long. 88° 08′ W, Elev. 8 m. A town in northeastern Yucatán; scrub forest and cultivated fields. Specimens were obtained at 8 kilometers north of town and at 8 kilometers north and 10 kilometers west of town.

Uxmal.—Lat. 20° 22′ N, Long. 89° 48′ W, Elev. 70 m. Mayan ruins on the highway between Mérida and Campeche. Specimens were obtained in the clearings around the ruins, which are situated in dense scrub forest.

Yokdzonot.—Lat. 20° 41′ N, Long. 88° 41′ W, Elev. 10 m. Town in dense scrub forest 10 kilometers west of Pisté. Collections were made at 3.5 kilometers east of town.

ANNOTATED LIST OF SPECIES

In the following accounts of the 96 species and subspecies (represented by 1774 specimens) that were collected in the Yucatan Peninsula by members of the two field parties from the University of Kansas, the localities from which those specimens were obtained are listed alphabetically within their respective states; the number after each locality signifies the number of specimens obtained there. For detailed comments on each of the localities, refer to the Gazetteer.

Amphibia

CAUDATA

Bolitoglossa mexicana mexicana Duméril, Bibron and Duméril

Yucatán: Cenote Seco, 1.

One specimen (71591) is a male having a snout-vent length of 49 mm., tail length, 38 mm., 11 costal grooves, 3.5 intercostal spaces between adpressed toes, and 7-9 vomerine teeth. In life the animal was dark brownish black above with diffuse orange-tan dorsolateral stripes. The top of the head was orange-tan with black flecks. The dorsal and lateral surfaces of the tail were orange-tan with black and cream-colored flecks. The flanks were black with tan flecks, and the ventral surfaces were dull brownish black with white flecks.

The taxonomy of the *mexicana-moreleti-mulleri-odonnelli* complex in *Bolitoglossa* is unsettled. Stuart (1963:17-18) recognized *Bolitoglossa moreleti* and *B. mulleri* as separate species and placed *B. odonnelli* in the synonymy of *B. mulleri*. Wake and Brame (1963:386) considered *B. mulleri* and *B. odonnelli* to be subspecies of *B. mexicana* and placed *B. moreleti* as a synonym of *B. mexicana mexicana*. Duellman (1963:220) committed a nomenclatural error by using the combination *B. moreleti mulleri*, instead of *B. mexicana mulleri* for specimens from southern El Petén. I now follow Wake and Brame in their allocation of names and refer the present specimen to *B. mexicana mexicana*.

The salamander was found beneath a log at the edge of the cenote. This is the first specimen reported from the northern part of the Yucatan Peninsula and represents a northward range extension of about 400 kilometers from Xunantunich, British Honduras, where the species was reported by Neill and Allen (1959:20) and Tikal, Guatemala, where it was reported by Stuart (1958:16).

SALIENTIA

Rhinophrynus dorsalis Duméril and Bibron

Campeche: Dzibalchén, 1; Escárcega, 12; Laguna Alvarado, 1.

The specimens from Escárcega were found on the ground at night after a rain. The individual from Dzibalchén was removed from a mouse trap, and the specimen from Laguna Alvarado was dug out from beneath a pile of debris in the dry season. This species was reported from Champotón and Tuxpeña, Campeche, by Gaige (1936:290), from Encarnación, Campeche, by Smith (1938:10), and from Chichén-Itzá, Yucatán, and from Xcopén, Quintana Roo, by Kellogg (1932:26). The species apparently is widespread in the peninsula and seems to avoid heavily forested areas.

Eleutherodactylus alfredi Boulenger

Quintana Roo: Pueblo Nuevo X-Can, 3.

The specimens were found in caves and are only tentatively assigned to this species, which is known to range from central Veracruz to western El Petén, Guatemala. The specimens currently are being studied in connection with a review of the *Eleutherodactylus alfredi* group by John D. Lynch at the University of Illinois.

Engystomops pustulosus Cope

Campeche: Escarcega, 1.

One individual was found beneath damp bark on the ground in December. No others were seen or heard. Apparently this species does not invade the wet forested regions of the southern part of the peninsula; it is unknown from the arid northern part of the peninsula. Smith (1938:11) reported specimens from Encarnación in southwestern Campeche.

Leptodactylus labialis (Cope)

Campeche: Chuina, 5; Escárcega, 4; Treinta y seis, 1. *Quintana Roo:* Isla Cozumel, 4.

All individuals were taken in the vicinity of water, such as a temporary pond at Escárcega, a reed-choked ditch on Isla Cozumel, and at permanent ponds at other localities. Gaige (1936:291) and Smith (1938:11) recorded the species from several localities in Campeche and Yucatán, and Maslin (1963:3) mentioned a specimen from Isla Cozumel.

Leptodactylus melanonotus (Hallowell)

Campeche: Champotón, 8; Chuina, 16; Treinta y seis, 4. *Quintana Roo:* Caobas, 1; Puerto Juárez, 2.

Like the preceding species, this frog was taken only in the vicinity of water. No breeding congregations were found. Although we did not find the species in the arid northern part of the peninsula in the state of Yucatán, Gaige (1936:291) recorded specimens from Yuncu and Pisté, Yucatán.

Bufo marinus (Linnaeus)

Campeche: Isla del Carmen, 1. *Quintana Roo:* Isla Cozumel, 1; Felipe Carrillo Puerto, 1. *Yucatán:* Chichén-Itzá, 1.

This large toad, which is common in most of the lowlands of México and Central America, was absent at most localities. Stuart (1958:7) suggested that the quasi-rainforest at Tikal precluded the presence there of *Bufo marinus*, which he intimated is an inhabitant of the scrub forest and savannas, but Duellman (1963:221) reported the species from the rainforests of southern El Petén. The present specimens all come from forested areas—quasi-rainforest at Felipe Carrillo Puerto, broad-leafed forest at the edge of a cenote at Chichén-Itzá, dense scrub forest on Isla Cozumel, and a coconut grove on Isla del Carmen.

Bufo valliceps valliceps Wiegmann

Campeche: Champotón, 14; Chuina, 7; Concepción, 1; Dzibalchén, 4; Escárcega, 30; Hopelchén, 3; Laguna Chumpich, 2; Laguna Silvituc, 13; Treinta y seis, 2. *Quintana Roo:* Caobas, 2; Felipe Carrillo Puerto, 5; Pueblo Nuevo X-Can, 15; Puerto Juárez, 3. *Yucatán:* Chichén-Itzá, 4; Pisté, 4; Yokdzonot, 1.

This toad is widespread on the peninsula, where it seems to be more abundant in the quasi-rainforest than in the scrub forest. In July, 1962, males were calling from shallow temporary ponds at Champotón and Escárcega, and large numbers of tadpoles were found in a shallow pool five kilometers south of Champotón. The dorsal ground color of the toads varies from yellowish tan to brown. No gray or reddish tan individuals like those reported from El Petén by Duellman (1963:221) were found.

Hyla loquax Gaige and Stuart

Campeche: Laguna Alvarado, 21; Laguna Silvituc, 2.

The series from Laguna Alvarado was obtained at night by Percy Clifton from rushes at the edge of open water in February; those from Laguna Silvituc were found by Clifton on plants at the edge of the water in December. In August, 1962, I heard this species calling from the midst of dense rushes at Felipe Carrillo Puerto, but no specimens were obtained. The only other records for the species from the peninsula are from Encarnación and Tres Brazos in southwestern Campeche (Smith, 1938:12).

Hyla microcephala martini Smith

Campeche: Escárcega, 15; Laguna Alvarado, 6; Xpujil, 2.

This species was breeding in a temporary pond at Escárcega on July 12, 1962, and it was heard, but individuals were not collected, at Felipe Carrillo Puerto, Quintana Roo. The other specimens were found at night on emergent vegetation in aguadas in the dry season. Barbour and Cole (1906:154) recorded the species (as *Hyla phlebodes*) from Chichén-Itzá, Yucatán.

Hyla picta (Günther)

Campeche: Escárcega, 16.

This small tree frog was breeding in a temporary pond on July 12, 1962. Although the species is known from scattered localities in El Petén, in the Yucatan Peninsula it is known only from southwestern Campeche.

Hyla staufferi Cope

Campeche: Champotón, 2; Escárcega, 11; Treinta y seis, 7. *Quintana Roo:* Isla Cozumel, 3.

Calling males were heard only on July 12, 1962, at a temporary pond at Escárcega, Campeche; others were sitting on vegetation at night. Apparently this small tree frog does not occur in the arid northern part of the peninsula, but it is widespread in the mesic parts of the peninsula.

Of the three specimens that we obtained on Isla Cozumel, two (71710-1) are recently metamorphosed young having snout-vent lengths of 10.2 and 10.3 mm., collected on August 7, 1962. The other specimen (71311) is a gravid female obtained on the same date. Maslin (1963:6) stated that the vocal sacs were unpigmented in the two males that he obtained on Isla Cozumel. In all breeding males that I have seen alive from throughout the range of the species the vocal sac is bright yellow. Perhaps Maslin's specimens were not in breeding condition, or possibly males from Isla Cozumel differ from those in other parts of the range.

Phrynohyas spilomma (Cope)

Campeche: Champotón, 5; Escárcega, 4; Laguna Silvituc, 1: Treinta y seis, 3. *Quintana Roo:* Felipe Carrillo Puerto, 1; Puerto Juárez, 2.

One male was calling from a tree in the forest at Felipe Carrillo Puerto on August 16, 1962. In the rainy season individuals were on trees at night at Champotón, Escárcega, and Puerto Juárez. In the dry season individuals were beneath the outer sheaths of banana plants at Treinta y seis. A juvenile having a snout-vent length of 32 mm. was beneath a log about 60 meters from

Laguna Silvituc in February. On the basis of the localities recorded here and those listed by Duellman (1956:35) the distribution of this species apparently encompasses the entire peninsula.

Phyllomedusa callidryas taylori Funkhouser

Campeche: Escárcega, 5.

Breeding individuals were obtained at a temporary pond at Escárcega, and males were heard, but not collected, at Felipe Carrillo Puerto, Quintana Roo. The specimen reported as *Agalychnis moreleti* from Tuxpeña, Campeche, by Gaige (1936:292) is *P. callidryas taylori.* Other records for the peninsula are from Chichén-Itzá, Yucatán (Gaige, 1936:292). Specimens from Chichén-Itzá and Culuba, Yucatán, are in the Chicago Natural History Museum. Since this species typically inhabits the wet tropical forest, I suspect that its distribution in the northern part of the peninsula is restricted to the margins of cenotes.

Smilisca baudini (Duméril and Bibron)

Campeche: Champotón, 13; Chuina, 3; Dzibalchén, 19; Escárcega, 29; Hopelchén, 3; Isla del Carmen, 20; Treinta y seis, 1. *Quintana Roo:* Felipe Carrillo Puerto, 2; Isla Cozumel, 4; Pueblo Nuevo X-Can, 2; Puerto Juárez, 10. *Yucatán:* Chichén-Itzá, 3; Mérida, 1; Yokdzonot, 3.

This large tree frog is abundant throughout the peninsula. In the rainy season the distinctive call was heard nearly every night.

Triprion petasatus (Cope)

Campeche: Champotón, 1; Dzibalchén, 14; Escárcega, 4. *Yucatán:* Chichén-Itzá, 54; Dzibichaltún, 4; Mérida, 1; Muna, 1; Pisté, 5; Yokdzonot, 43.

The many examples of this bizarre casque-headed tree frog have been reported in detail by Duellman and Klaas (1964). The specimens from Campeche are from localities intermediate between those in the dry northern part of the peninsula and those in the savannas of El Petén to the south.

Gastrophryne elegans (Boulenger)

Campeche: Xpujil, 1.

One specimen having a snout-vent length of 22.5 mm. was obtained from submerged grass roots in a marsh in February. The only other records for the species in the peninsula are from Becán and Tres Brazos in southern Campeche. This frog apparently is restricted to forested areas; it is known from southern Veracruz and southern Campeche southward to the lowlands of northern Alta Verapaz, Guatemala.

Hypopachus cuneus nigroreticulatus Taylor

Campeche: Concepción, 1; Escárcega, 38; Laguna Alvarado, 1; Laguna Chumpich, 1. *Quintana Roo:* Felipe Carrillo Puerto, 1; Puerto Juárez, 1. *Yucatán:* Dzitás, 1.

No breeding congregations were encountered; instead, these frogs were found moving about on the ground at night in the rainy season and to a lesser extent in the dry season. This fossorial frog is widespread in the peninsula; numerous localities are listed by Gaige (1936:294), who discussed the species under the name *Hypopachus inguinalis,* and by Smith (1938:2 and 12).

Rana palmipes Spix

Campeche: Laguna Chumpich, 1.

The single specimen was found at night at the edge of the lake in January. The only other record for the species in the peninsula is Tres Brazos in southwestern Campeche (Smith, 1938:13).

Rana pipiens Schreber

Campeche: Chuina, 2; Hopelchén, 1; Laguna Silvituc, 3. *Quintana Roo:* Caobas, 1; Felipe Carrillo Puerto, 1; Puerto Juárez, 4. *Yucatán:* Chichén-Itzá, 2.

All individuals were at the edges of cenotes or aguadas, except one in a cave at Felipe Carrillo Puerto. The records presented here and by Gaige (1936: 294) and Smith (1938:13) indicate that the species is widespread in the peninsula.

Reptilia

TESTUDINES

Caretta caretta (Linnaeus)

Campeche: Isla Aguada, 1. *Quintana Roo:* Isla Mujeres, 1.

One skull was picked up on the beach at Isla Aguada, and a skeleton was found on the rocky southern shore of Isla Mujeres.

Chelonia mydas (Linnaeus)

Quintana Roo: Isla Cozumel, 1.

A single skull was found on the beach 3.5 kilometers north of San Miguel.

Eretmochelys imbricata (Linnaeus)

Quintana Roo: Isla Mujeres, 1.

A skull was found on the beach at the northern end of Isla Mujeres.

Kinosternon creaseri Hartweg

Campeche: Champotón, 1; Dzibalchén, 1. *Quintana Roo:* Pueblo Nuevo X-Can, 6. *Yucatán:* Pisté, 7.

Fifteen specimens of this distinctive species were obtained. The largest is a male having a carapace length of 121.5 mm. In all specimens the anterior lobe of the plastron is noticeably longer than the middle portion, and in all adults the length of the gular shield is more than half the length of the anterior plastral lobe. Of five juveniles having carapace lengths of 34.4 to 41.5 mm., three specimens have gular shields that are less than half the length of the anterior plastral lobe. In juveniles a middorsal keel and a pair of dorsolateral keels are evident. With increased size the gular shield becomes relatively longer, and the keels on the carapace diminish; consequently, only a middorsal keel is evident in adults. Ontogenetic differences also are apparent in the lateral notching of the upper beak. The notches are barely noticeable in juveniles and only moderately developed in small adults (carapace lengths of 80 to 100 mm.), whereas in large adults, especially males, the upper jaw is deeply notched. In coloration the present specimens are like those described

by Hartweg (1934:2), except that two individuals (70921-2) found in a solution cave have pale tan carapaces, pale creamy yellow plastrons, and pale grayish brown limbs and heads.

All specimens are from the subhumid part of the peninsula, where the aquatic habitat is restricted to cenotes. Farther south *Kinosternon creaseri* is replaced in the humid forest, where lakes and streams are present, by *K. acutum*, which has been reported from the peninsula only from Balchacaj, Campeche, under the name *Kinosternon berendtianum* by Smith (1938:20).

Kinosternon cruentatum Duméril and Bibron

Campeche: Dzibalchén, 3; Isla del Carmen, 1; Laguna Silvituc, 1; Xpujil, 1. *Quintana Roo:* Isla Cozumel, 10. *Yucatán:* Tizimín, 1.

Stejneger (1941:458) named *Kinosternon cruentatum consors* from Isla Cozumel and diagnosed the subspecies as differing from *K. cruentatum cruentatum* by having a narrower and lower shell and the anterior lobe of the plastron averaging shorter than the middle portion. Examination of the data presented in Table 1 shows that the average width of the shell, as compared with the length, is slightly less in specimens from Isla Cozumel than in the samples from the mainland. The height of the shell and the relative lengths of the plastral lobes are not noticeably different in specimens from Isla Cozumel. No notable differences in coloration exist between the insular specimens and those from various localities on the mainland. The absence of characters to distinguish the specimens from Isla Cozumel and the northern part of the Yucatan Peninsula from individuals from the rest of the range of the species makes it necessary to place the name *Kinosternon cruentatum consors* Stejneger, 1941 (based on specimens from Isla Cozumel), as a synonym of *K. cruentatum* Duméril and Bibron, 1851.

TABLE 1.—COMPARISON OF FOUR SAMPLES OF KINOSTERNON CRUENTATUM (MEANS ARE GIVEN IN PARENTHESES BELOW OBSERVED RANGES)

Area	N	Carapace width/ carapace length	Shell height/ carapace length	Anterior lobe/ middle lobe	Gular/ anterior lobe
Cozumel	10	61.1–68.5 (65.6)	40.5–45.8 (44.0)	1.00–1.18 (1.09)	52.2–63.5 (58.1)
Yucatán	1	69.9	38.9	1.09	48.9
Campeche	6	64.2–73.4 (67.9)	39.6–50.6 (44.1)	1.08–1.21 (1.15)	42.3–60.1 (50.5)
Veracruz	6	64.3–69.1 (67.2)	47.8–50.2 (49.1)	1.07–1.15 (1.12)	50.1–53.9 (52.1)

All specimens are adults; the largest is a female from Isla Cozumel having a carapace length of 127.7 mm.; the largest specimen from the mainland is a female from Dzibalchén having a carapace length of 126.4 mm. The largest male is from Dzibalchén and has a carapace length of 117.0 mm. Considerable variation is apparent in the plastral scutes. The relative length of the gular

to the length of the anterior plastral lobe is given in Table 1. In all specimens from the mainland the pectoral scutes are in contact at the midline, but in six of ten specimens from Isla Cozumel the pectorals are separated posteromedially by the humerals. One specimen from Isla Cozumel and the specimen from Isla del Carmen have the femoral scutes separated in the midline, whereas in all others these scutes are in contact. Usually the axillary and inguinal scutes are separated by the lateral part of the abdominal scute, but in one specimen from Isla Cozumel the axillary and inguinal scutes are in contact on both sides of the shell, and in one specimen from Dzibalchén the scutes are in contact on the left side only.

Some notable sexual dimorphism is noticeable in these turtles. In males the greatest height of the shell is at a point about two-thirds the length of the carapace, from which point the carapace slopes abruptly downward; a slight depression is present anteromesially in the posterior lobe of the plastron. In females the highest point of the shell is about at mid-length, and there is no depression in the plastron. In males the throat is marked with dense brown reticulations tending to enclose small cream-colored spots. The throat in females is a dusty cream-color with a median dark grayish brown streak. The lower beak on males is predominantly brown; that in females is predominantly cream colored.

All specimens came from aquatic or semi-aquatic situations. The individuals from Isla Cozumel were found buried in mud or dug in at the bases of clumps of cat-tails in a partly dried up marsh. The specimen from Tizimín was in a cenote; specimens from Campeche were in lakes or aguadas, except the shell from Isla del Carmen, which was in a coconut grove.

Kinosternon leucostomum Duméril and Bibron

Quintana Roo: Felipe Carrillo Puerto, 1.

A single male having a carapace length of 117.7 mm. was trapped in a deep aguada. The anterior lobe of the plastron has a length of 33.5 mm.; the middle lobe, 24.0 mm.; the gular scute, 15.7 mm. The only other record for the peninsula is that given by Smith (1938:21) for Becán, Campeche.

Staurotypus triporcatus (Wiegmann)

Campeche: Laguna Chumpich, 3.

Three small individuals having carapace lengths of 106, 117, and 147 mm. were obtained from a marshy lake. One of these (75118) is represented by a shell found on the shore. In the preserved specimens the top and sides of the head are black with many small, round, white spots.

Geoemyda areolata (Duméril and Bibron)

Campeche: Dzibalchén, 2; Laguna Silvituc, 1. *Quintana Roo:* Isla Cozumel, 17; Pueblo Nuevo X-Can, 2. *Yucatán:* Pisté, 3.

This terrestrial turtle seems to be abundant in the arid scrub forest in the peninsula, especially on Isla Cozumel, where 17 individuals were found on the forest floor after rains. Juveniles, of which the smallest has a carapace length of 56 mm., are colored like the adults.

Pseudemys scripta ornata (Gray)

Campeche: Laguna Chumpich, 2; Laguna Silvituc, 1. *Quintana Roo:* Felipe Carrillo Puerto, 2.

Five adults were obtained from aquatic habitats—one from a pond in a stream, one from a trap in a deep aguada, and three from marshy lakes.

Terrapene mexicana yucatana (Boulenger)

Campeche: Dzibalchén, 3. *Yucatán:* Pisté, 4.

The following measurements are for the largest male and largest female, respectively—carapace length 135, 146; carapace width 104, 110; height of shell 68, 82 mm. All specimens have four toes and claws on each hind foot, and all have a deeply notched upper beak. Two specimens from Pisté and two from Dzibalchén have predominately yellow plastrons with brown sutures. The plastrons in the other specimens are predominately dark brown with irregular yellow areas. The carapace varies from olive-tan to predominately dark brown with yellowish tan blotches. In life a typically colored specimen from Pisté had a yellowish tan head with black flecks; the beaks were pinkish tan, and the iris was yellow. The species has been recorded from Chichén-Itzá by Barbour and Cole (1906:147), Gaige (1936:304), and Smith (1939a: 17), and from Cobá, Quintana Roo, by Smith (1939a:17).

CROCODILIA

Crocodylus moreleti Duméril and Duméril

Campeche: Laguna Alvarado, 2; Laguna Silvituc, 1.

The specimen from Laguna Silvituc is a skull 217 mm. in length; one of the specimens from Laguna Alvarado is a skull 398 mm. long, and the other is a juvenile having a total length of 900 mm. The species was observed commonly at Laguna Chumpich and at Laguna Alvarado. Individuals were seen in aguadas at Treinta y seis and Xpujil. Smith (1938:21) reported specimens from Balchacaj, Becán, and Encarnación, Campeche.

SAURIA

Aristelliger georgeensis (Bocourt)

Quintana Roo: Isla Cozumel, 6; Isla Mujeres, 12.

On Isla Mujeres these geckos were observed on coconut palms and on houses at night. Males often were located by their voice, which consists of a low "chirp." The lizards are extremely wary; often only the beam from a flashlight would cause them to scurry up the trunk into the bases of the fronds. Captured individuals strenuously twisted their bodies, readily dropped their tails, and bit viciously. On Isla Cozumel most specimens were taken on palm trunks or houses, and one was caught in a snap trap set in the fork of a tree about one and one-half meters above the ground in dense scrub forest.

The largest female has a snout-vent length of 97.9 mm.; the largest male, 96.3 mm. In life adults are pale greenish gray with rusty brown reticulations. In preservative they are grayish brown with brown reticulations. A juvenile

(70037) having a snout-vent length of 26.4 mm. has the top of the head pale tan; this color extends to the base of the tail in the form of a broad middorsal stripe with irregular edges. The side of the head, flanks, and limbs are dark brown with white flecks. The tail is brown with four creamy tan rectangular blotches on the proximal third. The distal one-sixth of the tail is white (yellow in life).

Previously this species has been reported in México from Isla Cozumel; Maslin (1963:8) commented on specimens obtained there in 1959, and Peters (1953:231) recorded the species from Felipe Carrillo Puerto on the mainland.

Coleonyx elegans elegans Gray

Campeche: Escárcega, 1; Laguna Chumpich, 1; Xpujil, 5. *Quintana Roo:* Caobas, 1; Felipe Carrillo Puerto, 1; Pueblo Nuevo X-Can, 3; Puerto Juárez, 2. *Yucatán:* Chichén-Itzá, 1; Kikil, 3; Mérida, 1; Pisté, 5.

This noctural lizard seems to be abundant throughout the peninsula. Many specimens were observed on roads at night, at which time they are readily identified by their habit of arching the tail as they walk. Several were caught in mouse traps.

The largest specimen is a male having a snout-vent length of 92.5 mm. and a tail length of 78.8 mm. Noticeable ontogenetic change in coloration takes place. In juveniles (less than 40 mm. in snout-vent length) the dark bands on the dorsum are only slightly darker than the interspaces; the dark bands on the trunk are narrowly bordered by black, and the caudal bands are solid black. Individuals having snout-vent lengths of 50 to 60 mm. have distinct dark dorsal bands broadly bordered by black, and the median parts of the caudal bands are brown. In large individuals the dorsal bands usually are dark brown to black with pale brown centers; the interspaces are pale creamy tan. One specimen from six kilometers south of Mérida is distinctive in having a linear pattern consisting of a broad middorsal tan stripe bordered on each side by a narrower brown stripe, which is continuous with the postorbital stripe. The flanks are tan and marked with dark brown dashes and circles. This pattern resembles that mentioned for certain specimens from the Yucatan Peninsula by Klauber (1945:194).

Females collected on August 15, 1962, and on April 9, 1963, each contained two eggs. Klauber (1945:195) listed several localities for this species from the peninsula and a record for Isla Mujeres.

Sphaerodactylus glaucus glaucus Cope

Campeche: Chuina, 1. *Quintana Roo:* Puerto Juárez, 1.

A specimen from Chuina was found beneath debris on the savanna. It is typical of this subspecies; in life it was grayish brown above with a black nape spot. The belly was yellow; the underside of the tail was orange-red, and the eye was orange.

The specimen from Puerto Juárez (70057) was found in one of our tents. This specimen has a snout-vent length of 20.3 mm. and a tail length of 16.7 mm. In general appearance the color pattern is suggestive of S. *torquatus* Strauch, for a distinctive double black collar is present on the neck. A double black ring is present on the base of the tail, which was red in life. White spots are present on the elbows and knees; in this respect the coloration is like that of S. *glaucus glaucus*. The color pattern of this specimen combines pattern characters of S. *glaucus* and S. *torquatus*. Since the latter is known to

occur only on the Pacific slopes of the Isthmus of Tehuantepec, the possibility that the present specimen is a hybrid is highly unlikely. The specimen probably was not introduced from the West Indies, for I know of no species of *Sphaerodactylus* in the West Indies that has smooth, imbricate, dorsal scales and a color pattern like that described above. The various studies on the systematics and distribution of Middle American *Sphaerodactylus,* such as those by Taylor (1947), Smith and MacDougall (1954), and Smith and Alvarez del Toro (1962), strongly point out the need for a thorough review of these lizards. Consequently, I refrain from drawing any conclusions concerning the specimen from Puerto Juárez.

Two individuals resembling the specimen from Puerto Juárez were observed in the litter on the forest floor at Pueblo Nuevo X-Can, Quintana Roo. Gaige (1936:295) recorded *S. glaucus* from Tuxpeña, and Smith (1938:13) reported the species from Apazote, Balchacaj, and Encarnación, Campeche.

Thecadactylus rapicaudus (Houttuyn)

Quintana Roo: Pueblo Nuevo X-Can, 2. *Yucatán:* Cenote Seco, 1; Kikil, 3; Pisté, 1.

Specimens were obtained from crevices in walls of cenotes, in caves, and on tree trunks covered with loose bark. Some kind of close fitting cover is characteristic of the places where these lizards live. They are quick to take refuge beneath bark or in crevices; none was observed on the ground.

Anolis humilis uniformis Cope

Campeche: Laguna Alvarado, 2; Laguna Chumpich, 1.

Previously this lizard has not been definitely recorded from the peninsula. The present specimens were obtained by Clifton in quasi-rainforest in extreme southern Campeche.

Anolis lemurinus bourgeaei Bocourt

Campeche: Chuina, 4; Escárcega, 1; Laguna Alvarado, 1; Laguna Chumpich, 1. *Quintana Roo:* Felipe Carrillo Puerto, 1; Pueblo Nuevo X-Can, 4. *Yucatán:* Cenote Seco, 4; Chichén-Itzá, 1.

This anole was most frequently observed on trunks of large trees, where the lizards usually were less than two meters above the ground. One was on a log at Laguna Chumpich, and another was on the ground at the edge of a cenote at Pueblo Nuevo X-Can. At Cenote Seco and Chichén-Itzá the species was in islands of mesic forest around cenotes in the otherwise low xerophilous forest. The color of the dewlap in males varies from deep orange to scarlet.

Anolis limifrons rodriguezi Bocourt

Campeche: Champotón, 5; Chuina, 12; Dzibalchén, 7; Escárcega, 1; Isla del Carmen, 23; Treinta y seis, 1. *Quintana Roo:* Caobas, 1; Isla Cozumel, 11; Isla Mujeres, 1; Limones, 1; Pueblo Nuevo X-Can, 5. *Yucatán:* Pisté, 5.

This ubiquitous little anole is widespread in the drier parts of the peninsula, where by day individuals were found on bushes and branches of low trees and at night on bushes and tall grass.

Little variation was noted; all specimens have the characteristic pale transverse bands on the shanks; the dewlap in living males is pale yellowish orange.

Anolis sagrei sagrei Duméril and Bibron

Quintana Roo: Isla Mujeres, 15; Xcalak, 5.

The present specimens were studied with respect to the characters used by Duellman and Schwartz (1958:281). All specimens have the supraorbital semicircle series separated by one row of scales, the caudal crest well developed, and moderate-sized granular lateral scales. Males have an orange dewlap and dark gray throat. In life active males were dark brown with cream-colored flecks dorsally; some individuals changed to olive-tan with creamy-white lateral stripes. In all aspects of coloration and scutellation the specimens from Quintana Roo are like those from Cuba. I agree with Stuart (1963:22) in his hesitation to accept as valid the recognition of the Central American populations of this species as *Anolis sagrei mayensis,* as proposed by Smith and Burger (1949:407). The possibility of independent introductions from various populations in the West Indies and the resemblance of the mainland specimens to those from Cuba clearly indicate that the recognition of a separate subspecies in Central America is undesirable. Fugler (personal communication) reached the same conclusion after studying specimens from British Honduras, although Neill and Allen (1959:34 and 1962:80) refer specimens from British Honduras to *Anolis sagrei mayensis.*

We obtained specimens from fences and trunks of coconut palms by day on Isla Mujeres. Two individuals were sleeping on palm fronds at night. Smith (1938:3) reported the species from Progreso, Mérida, and Chichén-Itzá in Yucatán, and from Balchacaj, Ciudad del Carmen, and Panlao in Campeche.

Anolis sericeus ustus Cope

Campeche: Champotón, 6; Chuina, 4; Dzibalchén, 6; Isla del Carmen, 1; Laguna Alvarado, 1; Laguna Silvituc, 1. *Quintana Roo:* Isla Mujeres, 2; Pueblo Nuevo X-Can, 1. *Yucatán:* Yokdzonot, 1.

The small anoles inhabiting the Atlantic lowlands of northern Middle America and having large, keeled ventral scales and a yellowish orange dewlap with a central blue spot have been recognized as three distinct species—*A. sericeus, ustus,* and *kidderi.* Stuart (1955) distinguished the species by size of dorsal scales, rugosity of supraoculars and scales in the frontal depression, and contact or separation of the occipital plate from scales in the supraorbital semicircle series. Furthermore, according to Stuart (1955:28), *Anolis ustus* has more than 60 dorsal scales (counted along midline from axilla to groin) and *A. sericeus* on the Atlantic lowlands has fewer than 60.

In the specimens that we obtained from the peninsula and adjacent islands, considerable variation obtains in all of the characters listed by Stuart. One specimen from Isla del Carmen has 64 dorsals. Eighteen specimens from the mainland of Campeche have 57-67 (average 62.4) dorsals; of these only three specimens have fewer than 60 scales. All three are from Champotón and have 57, 58, and 58 dorsals (three others from that locality have 61, 62, and 62 dorsals). The single specimen from Yucatán has 65; one from Pueblo Nuevo X-Can has 60, and two from Isla Mujeres have 68 and 70 dorsals.

The scales in the frontal depression and the supraoculars are strongly keeled in the specimens from Isla del Carmen and from Champotón, usually strongly or moderately keeled in specimens from other localities in Campeche, and nearly smooth in specimens from Yucatán and northern Quintana Roo.

In most specimens from the peninsula the supraorbital semicircles are separated by one row of scales; in all three specimens from Chuina, in one of six from Dzibalchén, and in the single specimens from Laguna Silvituc and Yokdzonot and semicircles are in contact. In the specimen from Laguna Silvituc (74876) the occipital plate is in contact with the supraorbital semicircles, whereas in all other specimens the plate is separated from the semicircles by one to three rows of small scales.

Examination of a series of *Anolis sericeus* from Jesús Carranza in southern Veracruz (27230-45) shows that in this sample the head scales are strongly keeled, the supraorbital semicircle series are separated by two or three small scales, and the number of dorsal scales varies from 45 to 53 (average 48.2). Four specimens of *Anolis sericeus* from southern El Petén, Guatemala (55792-3, 59529-30), have 44 to 51 (average 47.5) dorsals. The semicircles are separated by two rows of scales in one specimen and by only one row in the other three. In all four specimens the head scales are slightly keeled.

On the basis of these data and Stuart's (1955) discussion of the variation in *Anolis sericeus*, I can see no justification for recognizing *Anolis ustus* as a species distinct from *Anolis sericeus*. A logical arrangement is the assignment of the peninsular populations to *Anolis sericeus ustus*. The validity of *Anolis kidderi* is questionable, for the variation in the head scales in this group of anoles is of sufficient magnitude that the contact or separation of the occipital plate and supraoculars might be within the range of intraspecific variation. Also, the rugosity of the head shields is variable. In the specimen from Laguna Silvituc the head scales are nearly smooth, but Smith (1938:14) reported a specimen of *A. kidderi* from Campeche having keeled head scales. Until a thorough study of the available specimens of this group of anoles is completed, I am considering the specimen from Laguna Silvituc (74876) to be *Anolis sericeus ustus*, not *Anolis kidderi*.

Individuals of *Anolis sericeus ustus* were found on bushes and branches of low trees by day and sleeping on bushes and tall grass at night. Detailed field studies are needed to determine the ecological relationships between this species and *Anolis limifrons rodriguezi*. In southwestern Campeche both species are found in the same habitat.

Anolis tropidonotus tropidonotus Peters

Quintana Roo: Limones, 1.

The single specimen was found in leaf litter in dense evergreen forest. Previous records for the peninsula are Chichén-Itzá (Barbour and Cole, 1906: 149, as *Norops yucatanicus*), and Encarnación and Becán, Campeche (Smith, 1938:14).

Basiliscus vittatus Wiegmann

Campeche: Champotón, 14; Chuina, 3; Dzibalchén, 4; Escárcega, 3; Laguna Alvarado, 1; Laguna Chumpich, 4; Laguna Silvituc, 4. *Quintana Roo:* Felipe Carrillo Puerto, 4; Isla Cozumel, 5; Pueblo Nuevo X-Can, 7; Puerto Juárez, 1. *Yucatán:* Kikil, 7; Pisté, 11.

Usually this lizard is found in the vicinity of ponds and streams, but throughout the xeric western coastal region and northern parts of the peninsula, where such aquatic habitats are lacking, individuals were found in dense scrub forest. Except for three specimens from Escárcega, the species is absent in our col-

lections from the southern part of the peninsula, but Smith (1938:15) reported the species from Balchacaj, Encarnación, Pital, and Tres Brazos, Campeche.

Corythophanes hernandezi (Wiegmann)

Quintana Roo: Pueblo Nuevo X-Can, 1.

This specimen was found on a tree trunk in the forest. The dorsal crest is broadly separated from the helmet. With the exception of the cream-colored labials and loreolabials, the side of the head is dark brown. The throat is boldly barred with dark brown.

Ctenosaura similis (Gray)

Campeche: Champotón, 16; Dzibalchén, 1; Isla Aguada, 13; Isla del Carmen, 7. *Quintana Roo:* Isla Cozumel, 3; Isla Mujeres, 6; Puerto Juárez, 3; Xcalak, 2. *Yucatán:* Kikil, 2; Pisté, 23; Sisal, 1; Uxmal, 1.

This large lizard is abundant in the subhumid parts of the peninsula, especially in rocky areas. Many large adults were observed on the rocky shore of the Gulf or Mexico just north of Champotón. Likewise, the lizards are abundant on the rocky southern shore of Isla Mujeres. Juveniles were common in the coconut groves on Isla del Carmen in early July, 1962, and at Isla Aguada on June 9, 1963.

Enyaliosaurus defensor (Cope)

Campeche: Dzibalchén, 1. *Yucatán:* Pisté, 2.

Two species of *Enyaliosaurus* have been recognized in the Yucatan Peninsula. The first of these is *Cachryx* (= *Enyaliosaurus*) *defensor* Cope (1866: 124) from "Yucatan." I have examined the three syntypes (U. S. National Museum 12282). The other named species is *Ctenosaura* (= *Enyaliosaurus*) *erythromelas* Boulenger (1886:241); his description was based on a living specimen of unknown provenance and illustrated in color. Barbour and Cole (1906:150) reported *E. defensor* from Chichén-Itzá (Museum of Comparative Zoology 7095) and thereby provided the first definite locality for the species. Smith (1938:15) reported *E. erythromelas* from Balchacaj, Campeche (University of Illinois 20327). Additional records from the peninsula are Mayapán (Chicago Natural History Museum 40708-15) and the specimens reported here for the first time in our collections from the peninsula.

The principal character used to distinguish *E. defensor* from *E. erythromelas* is the presence or absence of rows of small scales between the whorls of large spinous scales on the dorsal surface of the tail (Bailey, 1928:48). In their descriptions both Cope and Boulenger described the dorsum as black with a middorsal red area.

Examination of all known specimens from the Yucatan Peninsula reveals that all adults have a red middorsum that varies in color from brick red to brownish red; the scapular region is black. A living male from Pisté, Yucatán, had an orange throat, greenish gray sides of the head, tan belly, and olive-gray tail. Six of fourteen specimens from Yucatán lack small scales between the enlarged dorsal caudal whorls, whereas the two specimens from Campeche and eight specimens from Yucatán have one row of small scales present dorsally between the enlarged whorls, at least anteriorly. In these specimens the small scales border only the median and paramedian enlarged scales. All

specimens have seven spinous scales dorsally in each whorl, and the posterior edges of the spines are perpendicular to the axis of the tail, except those in the lateral row, which point slightly posteriorly.

TABLE 2.—COMPARISON OF CERTAIN CHARACTERISTICS IN THE FOUR SPECIES OF ENYALIOSAURUS

(MEANS GIVEN IN PARENTHESES BELOW THE OBSERVED RANGES)

Species and Number of Specimens	Dorsals	Femoral pores	Lamellae under 4th toe	Spines in 4th whorl	Tail/body
E. palearis (7)	62–69 (65.4)	14–17 (15.3)	28–37 (31.0)	11–13 (11.3)	1.61–1.77 (1.71)
E. quinquecarinatus (34)	65–86 (77.1)	11–14 (13.1)	27–31 (29.2)	11–13 (11.3)	1.40–1.56 (1.47)
E. clarki (38)	76–110 (89.3)	8–12 (10.2)	25–33 (28.7)	9–11 (9.2)	0.89–1.06 (0.97)
E. defensor (16)	74–86 (70.4)	12–19 (15.0)	22–31 (26.8)	7	0.84–0.93 (0.88)

On the basis of the accumulated material from the Yucatan Peninsula, together with a familiarity with the species occurring in other parts of Middle America, I consider *Ctenosaura erythromelas* Boulenger, 1886, to be a synonym of *Cachryx* (= *Enyaliosaurus*) *defensor* Cope, 1866.

Enyaliosaurus defensor seems to be the most advanced member of the genus. The tail is short and bears few large spines. In this respect the species is most closely approached by *Enyaliosaurus clarki* (Bailey), which has a slightly longer tail and 9 to 11 spines in each caudal whorl; the coloration of *E. clarki* consists of large tan or cream-colored blotches on an olive-brown to black dorsum (Duellman and Duellman, 1959). The other species in the genus (*E. palearis* and *E. quinquecarinatus*) are green or grayish green with black markings. The distinguishing characteristics of scutellation and proportions of the species in the genus are given in Table 2.

The largest specimen of *E. defensor* is a male from Dzibalchén having a snout-vent length of 138 mm. and an incomplete tail. Maximum sizes of males of the other species are all in excess of that measurement—*clarki,* 154; *quinquecarinatus,* 160; *palearis,* 182 mm. *Enyaliosaurus* doubtless is a derivative of *Ctenosaura,* all species of which are larger and have relatively longer tails with less well-developed spines than *Enyaliosaurus.* The evolutionary trend in *Enyaliosaurus* seems to have been towards smaller size with a relatively more robust tail having whorls of large spines. In this respect, *E. palearis* seemingly is primitive; *E. quinquecarinatus* is more advanced and probably is ancestral to the specialized species, *E. clarki* and *E. defensor.*

Iguana iguana rhinolopha Wiegmann

Campeche: Isla del Carmen, 3. *Quintana Roo:* Isla Cozumel, 1.

All specimens are juveniles; that from Isla Cozumel was sleeping on a bush on the night of August 7, 1962; those from Isla del Carmen were in a grassy

area in a coconut grove on June 9, 1963. Smith (1938:15) also recorded the species from Isla del Carmen; to my knowledge the species is unknown from the mainland of the peninsula, although I suspect that it occurs at least in southern Quintana Roo along the Río Hondo.

Laemanctus deborrei Boulenger

Quintana Roo: Caobas, 1.

One adult male having a snout-vent length of 117 mm. and a tail length of 471 mm. is typical of the species and represents the first record from the peninsula.

Laemanctus serratus Cope

Campeche: Champotón, 4; Dzibalchén, 1. *Yucatán:* Kikil, 5; Pisté, 1.

Previous workers have recognized two species of *Laemanctus* in the Yucatan Peninsula—*L. serratus* Cope, 1864, and *L. alticoronatus* Cope, 1865. Boulenger (1885:105) distinguished the two species as follows: *L. serratus*—57-61 scales around midbody, a white streak from eye to the forelimb and from axilla to groin, a white spot on each side of the base of the tail; *L. alticoronatus*—45-51 scales around midbody, no white streak along flanks, but a white spot in front and another behind thigh. Barbour and Cole (1906:149) referred a specimen from Chichén-Itzá to *L. alticoronatus;* the specimen has 55 scales around the body, no white streaks on neck or flanks, and no white spots on the base of the tail or in front of the thighs. The authors stated: "This specimen seems ideally intermediate between the two species [*alticoronatus* and *serratus*], but with only one specimen definite conclusions are unreasonable." Gaige (1936:296) referred three specimens from Chichén-Itzá and three from Champotón to *L. serratus;* she gave the number of scales around midbody as 49, 53, and 58 for the specimens from Chichén-Itzá, 52, 57, and 61 for those from Champotón and stated: "The range of scale counts bridges the gap between those listed by Boulenger for *serratus* (57-61) and *alticoronatus* (45-51), and it seems possible that a larger series might prove that the two species are identical." Maslin (1963:9) reported on two specimens from Chichén-Itzá and one from Pisté but did not give scale counts or critical comments on coloration that serve to distinguish the two described species.

The eleven specimens that we obtained in the peninsula substantiate the suspicions expressed by Gaige and Barbour and Cole. In the 19 specimens recorded in the literature or collected by us the average number of scales around the body is 53.8; the variation is as follows (number of specimens in parentheses): 48 (1), 49 (1), 51 (3), 52 (4), 53 (1), 54 (1), 55 (1), 56 (2), 57 (2), 58 (1), 59 (1), 61 (1). If the specimens are arranged geographically from north to south, the following results are obtained (number of specimens in parentheses after locality and average number of scales in parentheses after observed range): Kikil (5), 48-56 (51.8); Chichén-Itzá and Pisté (6), 49-58 (53.3); Dzibalchén (1), 57; Champotón (7), 51-61 (55.4).

In coloration, several specimens lack the white spots at the base of the tail; these include two of five specimens from Kikil, one of five from Chichén-Itzá, and the one from Pisté. The white stripe on the head is lacking in one specimen from Chichén-Itzá and in the specimen from Pisté. In most specimens having a white spot in the groin, the spot is confluent with the lateral stripe. One individual from Chichén-Itzá, two from Kikil, and the specimen from Pisté lack spots in the groin.

On the basis of the above analysis of variation in scutellation and coloration and the lack of other features by which to distinguish two species of *Laemanctus* in the peninsula, I consider *Laemanctus alticoronatus* Cope, 1865, to be a synonym of *Laemanctus serratus* Cope, 1864.

All specimens were found in bushes and trees, where by night they were most conspicuous. In life the iris is yellow. The largest specimen is a female having a snout-vent length of 123 mm. and a tail length of 441 mm. Of four juveniles obtained at Kikil, the smallest has a snout-vent length of 55 mm. and a tail length of 204 mm.

Aside from the specimens listed above, the only other record for the peninsula is from Oxpemul, Campeche (Smith, 1938:15).

Sceloporus chrysostictus Cope

Campeche: Champotón, 16; Chuina, 13; Concepción, 1; Dzibalchén, 13; Isla Aguada, 9; Isla del Carmen, 8; Laguna Chumpich, 1; Laguna Silvituc, 5. *Quintana Roo:* Felipe Carrillo Puerto, 2; Isla Mujeres, 25; Pueblo Nuevo X-Can, 26; Puerto Juárez, 17; Xcalak, 1. *Yucatán:* Cenote Seco, 2; Kikil, 17; Pisté, 75; Sisal, 9.

This terrestrial lizard occurs throughout the peninsula, but seems to attain its greatest abundance in the scrub forest. Perhaps the fact that the lizards are more readily observed in the scrub forest than in the quasi-rainforest accounts for this impression, but careful observations in both habitats suggest that the species is not abundant in the mesic forest. The absence of the species on Isla Cozumel is unexpected.

Most individuals were basking in patches of sunlight on the forest floor or in open rocky areas. On the southern end of Isla Mujeres the species was in an open grassy area, where the lizards sought refuge in large clumps of *Opuntia*. On the coastal strand at Sisal the lizards were in an *Opuntia-Uniola* association.

TABLE 3.—VARIATION IN SIX SAMPLES OF SCELOPORUS CHRYSOSTICTUS (DATA FOR MALES ONLY; MEANS GIVEN IN PARENTHESES AFTER OBSERVED RANGES)

Locality	N	Dorsal scales	Femoral pores
Isla Mujeres	18	47–52 (48.9)	14–17 (15.2)
Puerto Juárez	13	43–50 (45.5)	13–16 (13.8)
Pisté	20	42–49 (44.8)	13–16 (14.3)
Dzibalchén	12	43–49 (45.6)	12–15 (13.5)
Chuina	13	43–50 (46.5)	12–15 (12.9)
Isla Aguada	9	44–52 (46.5)	13–16 (14.8)

Specimens from each of six localities were studied with regard to variation in scutellation. Of the characters studied, only the numbers of femoral pores and dorsal scales varied noticeably (Table 3). Most specimens have five enlarged supraoculars; three specimens from Isla Mujeres have six, and two specimens from Pisté and three from Chuina have four supraoculars. The

largest specimen is a male from Isla Mujeres and has a snout-vent length of 62 mm. and an incomplete tail 88 mm. in length. The largest female is from Puerto Juárez and has a snout-vent length of 54 mm. and a tail length of 96 mm. The smallest juvenile is from Puerto Juárez and has a snout-vent length of 20.5 mm. and a tail length of 33 mm. Maslin (1963:14) presented an excellent description of the colors in life and pointed out the marked sexual dimorphism in color and pattern.

Aside from the localities listed by Smith (1939b:299), Maslin (1963:14) reported the species from 9 kilometers north of Mérida and from Pisté, Yucatán.

Sceloporus cozumelae Jones

Quintana Roo: Isla Cozumel, 11; Isla Mujeres, 9; Puerto Juárez, 14. *Yucatán:* Sisal, 26.

This small terrestrial lizard is most frequently found on the white sand beaches where there are outcroppings of rock amidst sparse vegetation, but on the south end of Isla Mujeres the lizards were found in an open grassy area on rocky soil. Maslin (1963:13) described the colors in life, and Smith (1939b:249) discussed the variation in scutellation between individuals from the northern coast of Yucatán and those from Isla Cozumel. He showed that minor differences exist in the head scales and in the numbers of femoral pores (average of 7.3 on Isla Cozumel and 8.8 in Yucatán) and dorsal scales (average of 61.4 on Isla Cozumel and 58.9 in Yucatán). An analysis of the numbers of femoral pores and dorsal scales in specimens from four localities

Table 4.—Variation in Four Samples of Sceloporus cozumelae (Data for Males Only; Means Given in Parentheses After Observed Ranges)

Locality	N	Dorsal scales	Femoral pores
Sisal	19	48–53 (49.8)	8–10 (8.9)
Puerto Juárez	11	48–56 (51.6)	7–8 (7.7)
Isla Mujeres	9	52–56 (53.5)	7–9 (7.7)
Isla Cozumel	11	47–53 (49.3)	8–10 (8.8)

reveals that the variation does not seem to be correlated with geography (Table 4). In these characters the specimens from the most distant localities are more nearly alike than are the others.

The largest male has a snout-vent length of 59 mm. and the largest female, 48 mm. The smallest juvenile has a snout-vent length of 23 mm. and a tail length of 32 mm.

Sceloporus lundelli gaigeae Smith

Campeche: Chuina, 1; Dzibalchén, 7; Treinta y seis, 1. *Quintana Roo:* Pueblo Nuevo X-Can, 1. *Yucatán:* Pisté, 8.

All specimens have some form of a broad white stripe on the posterior surface of the thigh; faint, narrow, transverse dark bands are present on the dor-

sum in some individuals. The specimen from Treinta y seis apparently is the southernmost record for this subspecies, for Smith (1939b:71) referred specimens from Balchacaj, Campeche, to *S. lundelli lundelli*.

All specimens were found on tree trunks; some individuals were observed to ascend the trunks to limbs at least 20 meters above the ground.

Eumeces schwartzei Fischer

Campeche: Dzibalchén, 2. *Quintana Roo:* Pueblo Nuevo X-Can, 2. *Yucatán:* Pisté, 6.

All specimens of this widespread skink were found on the forest floor. Several individuals were observed to take refuge in holes or cracks in the limestone.

Mabuya brachypoda Taylor

Campeche: Champotón, 1; Isla Aguada, 1. *Quintana Roo:* Isla Cozumel, 3; Isla Mujeres, 1. *Yucatán:* Kikil, 1; Pisté, 3.

All specimens were found in open and relatively dry situations.

Scincella cherriei ixbaac Stuart

Quintana Roo: Pueblo Nuevo X-Can, 1.

A female having 60 dorsal scales arranged in 25 rows at midbody, a snout-vent length of 43 mm., and an incomplete tail 32 mm. in length was found in the leaf litter on the forest floor.

Ameiva undulata gaigeae Smith and Laufe

Campeche: Champotón, 6; Chuina, 2; Dzibalchén, 10; Escárcega, 5; Isla Aguada, 3; Laguna Chumpich, 3. *Quintana Roo:* Caobas, 2; Felipe Carrillo Puerto, 4; Isla Mujeres, 4; Limones, 1; Pueblo Nuevo X-Can, 4; Xcalak, 2. *Yucatán:* Cenote Seco, 3; Kikil, 5; Mérida, 1; Pisté, 42; Sisal, 1.

All adults have 12 or more pale blue vertical bars on the otherwise dark brown flanks and two rows of enlarged preanal scales. The specimens from Laguna Chumpich are juveniles that lack the adult color pattern used to distinguish *A. undulata gaigeae* and *A. undulata hartwegi;* the one adult from Xcalak has 13 vertical bars and is assignable to *A. undulata gaigeae*. Apparently the range of this subspecies includes all of the peninsula, except for the extreme southwestern part of the mainland just east of Laguna de Términos, where Smith and Laufe (1946:39) reported intergrades between *A. undulata gaigeae* and *A. u. hartwegi*.

Maslin (1963:16) described the coloration of specimens from Pisté, Yucatán, and commented on the two distinctive colors of throats in adult males—orange-red in some and bright lemon yellow in others. Of the males that we obtained at Pisté, approximately one half of the specimens have orange throats and the others yellow. Specimens from Escárcega, Champotón and Pueblo Nuevo X-Can have orange throats. Some males from Felipe Carrillo Puerto have orange throats, others have yellow. On the basis of this sample dichromatic throat color seems to occur in a broad area in the peninsula. Examination of other aspects of coloration and of scutellation revealed no differences between the specimens differing in the color of the throat.

All specimens were found in shaded areas. Since the species occurs on Isla

Mujeres, where dense forest is restricted to a small area in the middle of the island, the absence of *Ameiva* in the dense forest on Isla Cozumel was unexpected.

Cnemidophorus angusticeps angusticeps Cope

Campeche: Champotón, 13; Dzibalchén, 5. *Quintana Roo:* Felipe Carrillo Puerto, 10; Pueblo Nuevo X-Can, 15. *Yucatán:* Kikil, 14; Pisté, 56; Sisal, 24.

This lizard is abundant in scrub forest and savanna and avoids the mesic broad-leafed forest. Only along the Gulf coast at Sisal was the species found on the sandy coastal strand, a habitat occupied by *Cnemidophorus cozumelus* at Xcalak, Puerto Juárez, and on the off-shore islands. The specimens obtained on the coastal strand are pale and have a noticeably different pattern than specimens from inland areas. These specimens are being included in a study of the distribution and variation in the species by Clarence J. McCoy, Jr. and Kathleen Beargie at the University of Colorado Museum.

Cnemidophorus cozumelus cozumelus Gadow

Campeche: Isla del Carmen, 7. *Quintana Roo:* Isla Cozumel, 29; Xcalak, 4.

The specimens from Xcalak on the Caribbean coast of extreme southeastern Quintana Roo help to fill the distributional gap between the localities on Isla Cozumel and Ramate, El Petén, Guatemala, as shown by McCoy and Maslin (1962:621). The seven specimens from Isla del Carmen substantiate the sympatric occurrence on the island with *C. deppei deppei,* as first reported by McCoy and Maslin (1962:622). All of our specimens were obtained on sandy coastal strand sparsely covered with grass and shaded by coconut palms.

McCoy and Maslin (1962:622) stated that the number of granules around midbody in 76 specimens from Isla de Cozumel varied from 100 to 119 (average 107.0) and that 89.5 per cent of 238 specimens had two, three, or four accessory frontoparietals. These authors had three specimens from Isla del Carmen, and those specimens had 97, 98, and 103 granules around midbody and 3, 5, and 6 accessory frotoparietals. From the combined data given by McCoy and Maslin and those obtained from our specimens from Isla del Carmen, the variation in number of granules around midbody in ten specimens is 87 to 103 (average 95.1). Of the seven specimens that we obtained on the island, six have three accessory frontoparietals, and one specimen has only one accessory scute. Two specimens have the frontoparietals partially fragmented anteriorly. The four specimens from Xcalak have 94 to 98 (average 96.2) granules around midbody. Two of these specimens have three accessory frontoparietals; one has one, and one lacks accessory scutes.

The number of granules around midbody is much lower in samples from the southern part of the peninsula (Isla del Carmen and Xcalak) than in specimens from the north (Isla Cozumel), but four specimens from Ramate, El Petén, Guatemala, have 101 to 108 (average 105.0) granules (Duellman and Wellman, 1960:37).

Cnemidophorus cozumelus rodeki McCoy and Maslin

Quintana Roo: Isla Mujeres, 7; Puerto Juárez, 2.

These pallid specimens agree with the description of the subspecies given by McCoy and Maslin (1962:624); all were found on coastal strand.

SERPENTES

Boa constrictor imperator Daudin

Campeche: Champotón, 1; Chuina, 1; Dzibalchén, 1; Escárcega, 3. *Quintana Roo:* Pueblo Nuevo X-Can, 1; Puerto Juárez, 1. *Yucatán:* Pisté, 3; Sisal, 1.

Boas were found throughout the peninsula, except in southeastern Campeche and southern Quintana Roo, where the species probably occurs. Most specimens were found on roads at night, but one was found beneath a bush on the coastal strand at Sisal at mid-day.

Typhlops microstomus Cope

Yucatán: Pisté, 2.

One female (70816) has a total length of 337 mm.; in life the snake was uniform pinkish tan above and below, and the eye was not visible. The other specimen, a juvenile having a length of 192 mm., was the same color, but the eye was barely visible.

Coniophanes imperialis clavatus (Peters)

Campeche: Champotón, 1; Escárcega, 2; Laguna Alvardo, 1; Laguna Chumpich, 1.

The belly was dull red in life; the middorsal stripe is noticeable in the specimen from Champotón; in the others the stripe is barely evident. Four individuals were found on the ground at night; one individual was trying to engulf a mangled, dead *Phrynohyas spilomma*. One individual was found in forest litter at Laguna Alvarado on March 1, 1963.

Coniophanes meridianus Schmidt and Andrews

Campeche: Dzibalchén, 1.

The single specimen from dense scrub forest at Dzibalchén agrees with the descriptions of the species given by Schmidt and Andrews (1936:179) and Andrews (1937:359). The chin, throat, and labials are cream-color with black flecks; the head and nape are dark brown. A cream colored stripe extends from the top of the eye onto the second upper temporal. A series of dark brown dashes form an interrupted stripe on the upper 3rd and lower 4th rows of dorsal scales. A row of dashes exists middorsally on the anterior three-fourths of the body, which is pale tan and darkest middorsally. The specimen is a male having a body length of 198 mm., a tail length of 105 mm., and the following scale formula: $17 \frac{7+8\ (73)}{7+8\ (74)}$ 15 (123) + 90 caudals.

Coniophanes schmidti Bailey

Yucatán: Pisté, 3.

Two specimens (70830-1) have the typical color pattern of the temporal stripe continuous with the dorsolateral stripe, whereas the other specimen (70829) is pallid dorsally. Its temporal stripes terminate on the nape, and the dorsolateral stripes begin at the level of the 25th ventral. This specimen is a female having 170 ventrals and 95 caudals. The other specimens are males having 161 and 167 ventrals and 104 and 103 caudals.

Conophis lineatus concolor Cope

Campeche: Chuina, 1. *Yucatán:* Kikil, 2; Pisté, 5; Uxmal, 1.

All of the specimens from Yucatán agree with the definition of the subspecies *C. l. concolor* as given by Wellman (1963:270). Aside from the localities mentioned above, one individual was observed on the coastal strand at Sisal, Yucatán, and another was seen in scrub forest on Isla Mujeres, Quintana Roo.

The specimen from the savanna at Chuina, Campeche, is an intergrade between *C. l. lineatus* to the south and west and *C. l. concolor* to the north. The specimen is a male having 163 ventrals and 68 caudals. The tips of the scales in the seventh dorsal scale rows are black throughout the length of the body and onto the base of the tail. The tips of most of the scales in the fourth dorsal rows on the anterior two-thirds of the body also are black. These interrupted stripes correspond to the lateral and dorsolateral stripes that are continuous in *C. l. lineatus* (Wellman, 1963:268), which also has continuous stripes on the first scale rows.

Dipsas brevifacies (Cope)

Quintana Roo: Puerto Juárez, 1. *Yucatán:* Pisté, 2.

The range of variation in scutellation exhibited by these specimens is within that given by Peters (1960:40). In life the body is black above and below with broad orange rings that are palest ventrally. This coloration is in contrast with that described for a specimen from Chichén-Itzá by Schmidt and Andrews (1936:175), who stated: "In life the light body-bands were bittersweet pink alternating with black, with a flame scarlet neck-band."

All specimens were found on roads at night.

Dryadophis melanolomus melanolomus (Cope)

Campeche: Dzibalchén, 2. *Quintana Roo:* Felipe Carrillo Puerto, 2; Pueblo Nuevo X-Can, 1. *Yucatán:* Mérida, 1; Pisté, 1.

All specimens have the dorsal scales edged with black. In some individuals the amount of black on the scales in the first, second, fourth, and fifth dorsal rows is so much reduced that the dark upper edges of the scales in the third row give the illusion of a lateral dark stripe. All individuals were found in scrub forest by day.

Drymobius margaritiferus margaritiferus (Schlegel)

Campeche: Champotón, 1. *Quintana Roo:* Dziuché, 1; Felipe Carrillo Puerto, 1.

All individuals of this species were found in forested areas; to my knowledge *Drymobius* avoids the arid tropical scrub forest on the northern end of the peninsula.

Elaphe flavirufa phaescens Dowling

Quintana Roo: Puerto Juárez, 2. *Yucatán:* Chichén-Itzá, 1.

Data from these specimens serve to supplement the description of this subspecies given by Dowling (1952), who based his description on one adult male and four small females. The two specimens from Puerto Juárez (70850-1) are adult females having 30 and 29 body blotches, 260 and 262 ventrals, 60 +

and 96 caudals, 2 and 3 rows of smooth scales at midbody, body lengths of 1435 and 1100 mm.; the latter has a tail/body length ratio of 21.2 per cent. In these specimens the dorsal ground color in life was a dull yellowish gray, and the blotches were dark chocolate brown. The specimen from Chichén-Itzá is a half-grown male having 31 body blotches, 260 ventrals, 99 caudals, 5 rows of smooth scales at midbody, a body length of 657 mm., and a tail/body ratio of 23.3 per cent. In life the dorsal ground color was yellowish tan; the dorsal blotches were reddish brown outlined with dark brown. The iris was pale grayish tan.

All specimens were found active at night.

Elaphe triaspis triaspis (Cope)

Quintana Roo: Felipe Carrillo Puerto, 1. *Yucatán:* Pisté, 5.

Five specimens from Pisté have 49-55 (average 52) dorsal body blotches, and one specimen from Felipe Carrillo Puerto has 52 blotches. These are well within the range of variation given for this subspecies by Dowling (1960: 72). The dorsal ground color in three juveniles from Pisté is orange-tan; the blotches are solid dark brown. Adults have a grayish tan ground color and brown blotches with pale centers.

Ficimia publia Cope

Campeche: Chuina, 1. *Yucatán:* Pisté, 1.

The specimen from Pisté is an adult female having 22 dorsal body blotches that are about equal in length to the middorsal interspaces, 2-2 postoculars, and no internasals. The specimen from Chuina is a small male having 31 dorsal body blotches that are about equal in length to the middorsal interspaces, 1-2 postoculars, and no internasals. The female is orange-tan with brown blotches having pale brown centers, whereas the small male has a yellowish tan ground color with solid dark brown blotches.

Smith (1947:411) named and diagnosed *Ficimia publia taylori* on the basis of two specimens from San Lorenzo, Veracruz. He stated that the Veracrucian subspecies was distinctive in ". . . having a reduced number (about 30) of large blotches about as wide as the interspaces on the back, differing from [*publia*] usually in lacking internasals and having only one postocular on each side." The present specimens do not seem to fit the pattern of geographic variation described by Smith; consequently, until additional material is available to permit a better definition of subspecies, I prefer to use only the binomial.

Imantodes cenchoa leucomelas Cope

Campeche: Chuina, 1.

One specimen of this widespread species was obtained by Clifton from a resident of Chuina.

Imantodes tenuissimus Cope

Yucatán: Pisté, 2.

Both specimens are females having 242 and 246 ventrals, 142 and 146 caudals, 41 and 43 dorsal dark blotches on the body, and 31 and 33 blotches

on the tail. The dark brown dorsal blotches extend laterally onto the edges of the ventrals, and the pale creamy tan interspaces are shorter than the blotches middorsally.

One specimen was brought to us by a local resident; the other was found on a road at night.

Lampropeltis doliata blanchardi Stuart

Quintana Roo: Pueblo Nuevo X-Can, 1. *Yucatán:* Pisté, 1.

A large male from Pisté has a body length of 1094 mm. and a tail length of 188 mm. Both specimens were found at night.

Leptodeira frenata malleisi Dunn and Stuart

Campeche: Escárcega, 1; Isla del Carmén, 1. *Quintana Roo:* Felipe Carrillo Puerto, 2; Isla Cozumel, 1.

The coloration of these specimens agrees with the analysis of geographic variation in the number and color of dorsal body blotches presented by Duellman (1958:60). The number of dorsal body blotches is: Isla del Carmen, 28; Escárcega, 26; Felipe Carrillo Puerto, 24 and 26; Isla Cozumel, 26. One specimen from Felipe Carrillo Puerto (70868) has solid dark brown blotches; the others have blotches that are pale brown in the center.

All specimens were found on roads at night.

Leptodeira frenata yucatanensis (Cope)

Yucatán: Pisté, 1.

The single female has 24 brown blotches on the body; the blotches are edged with black. In life the dorsal ground color was pinkish brown, and the venter was a rosy cream color.

Leptophis mexicanus mexicanus Duméril, Bibron, and Duméril

Campeche: Escárcega, 2.

These two specimens have narrow lateral dark stripes present posteriorly only on the upper part of the second and lower part of the third rows of scales. One specimen is a male having 159 ventrals; the other is a female having 168. Oliver (1948:214) considered three specimens from Balchacaj in southwestern Campeche to be intergrades between *L. mexicanus mexicanus* and *L. m. yucatanensis;* he stated that those specimens have the color pattern of *yucatanensis* (broad lateral dark stripe) and the low number of ventrals characteristic of *mexicanus.* The two specimens from Escárcega have color patterns typical of the subspecies *mexicanus;* furthermore, the numbers of ventrals are within the range of variation in that subspecies as reported by Oliver (1948:201).

Leptophis mexicanus mexicanus Oliver

Campeche: Dzibalchén, 3. *Yucatán:* Kikil, 1; Pisté, 7.

Four males have 162-165 (average 163.2) ventrals, and six females have 163-171 (average 166.6) ventrals. All specimens have a broad lateral dark stripe encompassing all of the third and adjacent parts of the second and fourth rows of scales posteriorly. A juvenile having a body length of 280 mm. and a tail length of 170 mm. is colored like the adults.

Ninia sebae morleyi Schmidt and Andrews

Campeche: Chuina, 1.

This male has 143 ventrals and 50 caudals; in these characters it is typical of *Ninia sebae morleyi* as defined by Schmidt and Rand (1957:76). Posterior to the black nuchal band, the body is uniform red above, except for the black tips of the scales and the presence of a pair of black spots on the sixth and seventh scale rows at the level of the ninth ventral. The snake was found beneath a pile of palm fronds.

Oxybelis aeneus auratus (Bell)

Yucatán: Pisté, 1.

According to Bogert and Oliver (1945:388), in *Oxybelis aeneus aeneus* the diameter of the eye is more than the length of the internasal, whereas in *O. aeneus auratus* the diameter of the eye is less than the internasal. The present specimen, a male, has an internasal:eye ratio of 1:1.2 and thus is assignable to the subspecies *O. a. auratus.*

Oxybelis fulgidus (Daudin)

Campeche: Crucero, 1; Dzibalchén, 1. *Yucatán:* Kikil, 1.

All specimens were found in scrub forest; the individual from Crucero was on a road during a hard rain in mid-afternoon.

Pliocercus andrewsi andrewsi Smith

Yucatán: Pisté, 1.

This female, brought to us by a local resident, has 126 ventrals and an incomplete tail, 5 black rings plus a black nuchal band, and 5 red rings on the body. The rings are narrowly separated by yellow. The black rings are 10 to 13 scales in length dorsally and 7 to 9 scales ventrally. The scales in the red rings have black tips; the temporal band, labials, and chin are creamy yellow.

Scaphiodontophis zeteki nothus Taylor and Smith

Yucatán: Pisté, 1.

This male provides the first record for the genus from the Yucatan Peninsula. The anterior two-thirds of the body has black, white, and red bands. The snout is black. The posterior one-third of the body is dull brown with a row of black spots on the vertebral row and fifth rows of scales. The belly is pale creamy yellow.

Sibon sanniola (Cope)

Campeche: Champotón, 1; Dzibalchén, 1. *Quintana Roo:* Felipe Carrillo Puerto, 1. *Yucatán:* Chichén-Itzá, 1; Dzitás, 1.

All specimens are typical of the species as defined by Peters (1960:187). In life the dorsum was rich pale brown with dark brown dorsal blotches narrowly outlined by creamy yellow. The specimen from Champotón extends the known range of the species into southwestern Campeche.

Spilotes pullatus mexicanus (Laurenti)

Campeche: Dzibalchén, 1; 78 km. E of Escárcega, 1. *Quintana Roo:* Puerto Juárez, 1. *Yucatán:* Pisté, 1.

Individuals of this species were found in scrub forest and in quasi-rain-forest. The specimen from 78 kilometers east of Escárcega was found in a tree.

Stenorrhina freminvillei Duméril, Bibron and Duméril

Yucatán: Pisté, 1.

This female has a body length of 508 mm. and a tail length of 81 mm. The belly is uniform creamy yellow; the dorsum is grayish brown, and the base of each scale is black. I follow Stuart (1963:117) in not recognizing the poorly distinguished subspecies.

Tantilla canula Cope

Campeche: Champotón, 1.

A female having 106 ventrals and 34 caudals provides the third known locality for this species on the peninsula. Previously the species has been definitely recorded only from Chichén-Itzá and Libre Unión, Yucatán. On each side the specimen has seven upper and six lower labials, one preocular, two postoculars, and two temporals. The general dorsal coloration is brown with a narrow middorsal creamy white line that is most distinct on the tail. The snout is creamy yellow, and the belly is white. The body length is 109 mm., and the tail length is 26 mm.

Tantilla cuniculator Smith

Yucatán: Pisté, 1.

The female has 147 ventrals, a body length of 163 mm., and an incomplete tail. It differs noticeably from the types (Smith, 1939a:32) in having the rostral broadly visible from above; the posterior edge of the rostral extends posteriorly and partly separates, the internasals. The dorsolateral light stripe is barely evident.

Thamnophis proximans rutiloris (Cope)

Quintana Roo: Isla Cozumel, 1.

One individual was obtained in a clump of mangroves, where it took refuge in a small hole in the ground.

Tropidodipsas fasciata fasciata Günther

Campeche: Hopelchén, 1.

A female was dead on a road at night; it has 183 ventrals, 68 caudals, 20 grayish white bands on the body, and 12 bands on the tail.

Tropidodipsas sartori sartori Cope

Campeche: Xpujil, 1. *Quintana Roo:* Pueblo Nuevo X-Can, 1. *Yucatán:* Peto, 2.

The specimen from Pueblo Nuevo X-Can was found in a cave; the others were found on roads at night.

Micrurus affinis alienus (Werner)

Campeche: Dzibalchén, 1.

The one female has 22 black rings on the body, 217 ventrals, and 38 caudals, of which the ten anteriormost are undivided. The individual, which was found in scrub forest, is typical of the subspecies *M. a. alienus* as defined by Schmidt (1936:212).

Micrurus affinis mayensis Schmidt

Yucatán: Pisté, 1.

This male was on a road at night; it has 14 black rings on the body, 189 ventrals, and 51 caudals, of which the 17 anteriormost are undivided. The specimen agrees with the description of *M. a. mayensis* (Schmidt, 1933:37), except in having a lower number of ventrals; Schmidt gave the range of ventrals in males as 195-203.

Agkistrodon bilineatus bilineatus Günther

Campeche: Champotón, 1. *Yucatán:* Pisté, 2.

These specimens, which were found at night in scrub forest, are being studied by Howard K. Gloyd at the University of Arizona.

Bothrops atrox asper (Garman)

Campeche: Xpujil, 1. *Quintana Roo:* Caobas, 2; Pueblo Nuevo X-Can, 2; Puerto Juárez, 1. *Yucatán:* Kikil, 1.

No large individuals were found, but small examples seemed to be abundant in various parts of the peninsula in both wet and dry seasons.

Bothrops yucatanicus (Smith)

Yucatán: Pisté, 2.

Two small individuals in life had pale yellow tails and a sharply defined creamy yellow middorsal stripe. One specimen contained a *Sceloporus chrysostictus.*

Crotalus durissus tzabcan Klauber

Campeche: Champotón, 3; Dzibalchén, 3; Escárcega, 1. *Quintana Roo:* Caobas, 1. *Yucatán:* Kikil, 1; Pisté, 3; Tizimín, 1.

Rattlesnakes were common in the scrub forest in the peninsula. Several individuals are large, the largest having a total length of 1688 mm. In small individuals the lateral body blotches are solid dark brown or black, and the middorsal diamond-shaped blotches are black with brown centers and narrowly outlined with creamy yellow. In large individuals the dorsal and lateral blotches are reddish brown or chocolate brown; the centers of the middorsal blotches are tan.

SUMMARY

Locality records are given for each of the 96 species and subspecies of amphibians and reptiles collected in the Yucatan Peninsula by field parties from the University of Kansas in 1962 and 1963. Five species (*Bolitoglossa mexicana mexicana, Eleutherodactylus*

alfredi, Anolis humilis uniformis, Laemanctus deborrei, and *Scaphiodontophis zeteki*) are recorded for the first time from the Yucatan Peninsula. Notable range extensions on the peninsula are recorded for many other species.

Detailed studies of certain species have resulted in the following taxonomic changes:

1.—*Kinosternon cruentatum consors* Stejneger, 1941, is considered to be invalid; consequently, all specimens from the peninsula are referred to *Kinosternon cruentatum* Duméril and Bibron, 1851.

2.—*Anolis ustus* Cope, 1864, is shown to be a subspecies of *Anolis sericeus* Hallowell, 1856.

3.—*Ctenosaura* (= *Enyaliosaurus*) *erythromelas* Boulenger, 1886 is shown to be the same as *Cachryx* (= *Enyaliosaurus*) *defensor* Cope, 1866.

4.—*Laemanctus alticoronatus* Cope, 1865, is placed in the synonymy of *Laemanctus serratus* Cope, 1864.

LITERATURE CITED

Andrews, E. W.
1937. Notes on snakes from the Yucatan Peninsula. Zool. Ser. Field Mus. Nat. Hist., 20:355-359, December 28.

Bailey, J. W.
1928. A revision of the lizards of the genus Ctenosaura. Proc. U. S. Nat. Mus., 73:1-58, pls. 1-36, September 26.

Bogert, C. M. and Oliver, J. A.
1945. A preliminary analysis of the herpetofauna of Sonora. Bull. Amer. Mus. Nat. Hist., 83:297-426, March 30.

Boulenger, G. A.
1885. Catalogue of the lizards in the British Museum (Natural History), 2nd Ed., vol. 2: xiii + 497 pp., pls. 1-24, November 15.
1886. Description of a new iguanoid lizard living in the Society's Gardens. Proc. Zool. Soc. London, p. 241, pl. 23.

Cole, L. J. and Barbour, T.
1906. Vertebrata from Yucatan. Reptilia, Amphibia, Pisces. Bull. Mus. Comp. Zool., 50:146-159.

Cope, E. D.
1866. Fourth contribution to the herpetology of tropical America. Proc. Acad. Nat. Sci. Philadelphia, 18:123-133.

Dowling, H. G.
1952. A taxonomic study of the ratsnakes, genus *Elaphe* Fitzinger. II. The subspecies of *Elaphe flavirufa* (Cope). Occ. Papers Mus. Zool. Univ. Michigan, 540:1-14, pl. 1, June 20.
1960. A taxonomic study of the ratsnakes, genus *Elaphe* Fitzinger. VII. The triaspis section. Zoologica, 45:53-80, pl. 1, August 15.

Duellman, W. E.
1956. The frogs of the hylid genus *Phrynohyas* Fitzinger, 1843. Misc. Publ. Mus. Zool. Univ. Michigan, 96:1-47, pls. 1-6, February 21.
1958. A monographic study of the colubrid snake genus *Leptodeira*. Bull. Amer. Mus. Nat. Hist., 114:1-152, pls. 1-31, February 24.
1963. Amphibians and reptiles of the rainforests of southern El Petén, Guatemala. Univ. Kansas Publ. Mus. Nat. Hist., 15:205-249, October 4.

DUELLMAN, W. E. and DUELLMAN, A S.
1959. Variation, distribution, and ecology of the iguanid lizard *Enyaliosaurus clarki* of Michoacán, Mexico. Occ. Papers Mus. Zool. Univ. Michigan, 598:1-10, pl. 1, February 16.

DUELLMAN, W. E. and KLAAS, L. T.
1964. The biology of the hylid frog *Triprion petasatus*. Copeia (2):308-321, June 30.

DUELLMAN, W. E. and SCHWARTZ, A.
1958: Amphibians and reptiles of southern Florida. Bull. Florida State Mus., 3:181-324, December 10.

DUELLMAN, W. E. and WELLMAN, J.
1960. A systematic study of the lizards of the *Deppei* group (genus *Cnemidophorus*) in Mexico and Guatemala. Misc. Publ. Mus. Zool. Univ. Michigan, 111: 1-80, pl. 1, February 10.

GAIGE, H. T.
1936. Some reptiles and amphibians from Yucatan and Campeche, Mexico. Carnegie Inst. Washington Publ. No. 457:289-304, February 5.

HARTWEG, N.
1934. Description of a new kinosternid from Yucatán. Occ. Papers Mus. Zool. Univ. Michigan, 277:1-2, January 2.

KELLOGG, R.
1932. Mexican tailless amphibians in the United States National Museum. Bull. U. S. Nat. Mus., 160:1-224, March 31.

KLAUBER, L. M.
1945. The geckos of the genus Coleonyx with descriptions of new subspecies. Trans. San Diego Soc. Nat. Hist., 10:133-216, March 9.

MASLIN, T. P.
1963. Notes on a collection of herpetozoa [*sic*] from the Yucatan Peninsula of Mexico. Univ. Colorado Studies, Biol., 9:1-20, February.

MCCOY, JR., C. J.
1963. Eumeces sumichrasti (Reptilia:Scincidae) in Quintana Roo, Mexico. Herpetologica, 19:224, September 11.

MCCOY, JR., C. J. and MASLIN, T. P.
1962. A review of the teiid lizard *Cnemidophorus cozumelus* and the recognition of a new race, *Cnemidophorus cozumelus rodecki*. Copeia (3):620-627, September 28.

NEILL, W. T. and ALLEN, R.
1959. Studies on the amphibians and reptiles of British Honduras. Publ. Res. Div. Ross Allen's Reptile Inst., Inc., 2:1-76, November 10.

NEILL, W. T. and ALLEN, R.
1962. Reptiles of the Cambridge Expedition to British Honduras, 1959-60. Herpetologica, 18:79-91, June 22.

OLIVER, J. A.
1948. The relationships and zoogeography of the genus *Thalerophis* Oliver. Bull. Amer. Mus. Nat. Hist., 92:157-280, pls. 16-19, November 22.

PAYNTER, JR., R. A.
1955. The ornithogeography of the Yucatán Peninsula. Peabody Mus. Nat. Hist., Bull. 9:1-347.

PETERS, J. A.
1953. Snakes and lizards from Quintana Roo, Mexico. Lloydia, 16:227-232, September.
1960. The snakes of the subfamily Dipsadinae. Misc. Publ. Mus. Zool. Univ. Michigan, 114:1-224, pls. 1-8, May 25.

SCHMIDT, K. P.
1933. Preliminary account of the coral snakes of Central America and Mexico. Zool. Ser. Field Mus. Nat. Hist., 20:29-40, December 11.
1936. Notes on Central American and Mexican coral snakes. Zool. Ser. Field Mus. Nat. Hist., 20:205-216, October 31.

Schmidt, K. P. and Andrews, E. W.
1936. Notes on snakes from Yucatán. Zool. Ser. Field Mus. Nat. Hist., 20:167-187, October 31.

Schmidt, K. P. and Rand, A. S.
1957. Geographic variation in the Central American snake Ninia sebae. Fieldiana. Zool., 39:73-84, October 31.

Smith, H. M.
1938. Notes on reptiles and amphibians from Yucatan and Campeche, Mexico. Occ. Papers Mus. Zool. Univ. Michigan, 388:1-22, October 31.
1939a. Notes on Mexican reptiles and amphibians. Zool. Ser. Field Mus. Nat. Hist., 24:15-35, January 30.
1939b. The Mexican and Central American lizards of the genus Sceloporus. Zool. Ser. Field Mus. Nat. Hist., 26:1-397, pls. 1-31, July 27.
1947. Notes on Mexican amphibians and reptiles. Jour. Washington Acad. Sci., 37:408-412, November 15.

Smith, H. M. and Alvarez del Toro, M.
1962. Notulae Herpetologicae Chiapasiae III. Herpetologica, 18:101-107, June 22.

Smith, H. M. and Burger, W. L.
1949. A new subspecies of Anolis sagrei from the Atlantic coast of tropical America. Anal. Inst. Biol., Mexico, 20:407-410.

Smith, H. M. and Laufe, L. E.
1946. A summary of the Mexican lizards of the genus *Ameiva*. Univ. Kansas Sci. Bull., 31:7-73.

Smith, H. M. and MacDougall, T.
1954. The status and origin of the geckos of the genus *Sphaerodactylus* on the Pacific slope of the Isthmus of Tehuantepec, Mexico. Herpetologica, 10:21-30.

Stejneger, L.
1941. Notes on Mexican turtles of the genus Kinosternon. Proc. U. S. Nat. Mus., 90:457-459, July 25.

Stuart, L. C.
1955. A brief review of the Guatemalan lizards of the genus *Anolis*. Misc. Publ. Mus. Zool. Univ. Michigan, 91:1-31, June 6.
1958. A study of the herpetofauna of the Uaxactun-Tikal area of northern El Peten, Guatemala. Contr. Lab. Vert. Biol., Univ. Michigan, 75: 1-30, June.
1963. A checklist of the herpetofauna of Guatemala. Misc. Publ. Mus. Zool. Univ. Michigan, 122:1-150, April 2.

Taylor, E. H.
1947. A review of the Mexican forms of the lizard genus *Sphaerodactylus*. Univ. Kansas Sci. Bull., 31:299-309, November 1.

Wake, D. B. and Brame, Jr., A. H.
1963. The status of the plethodontid salamander genera *Bolitoglossa* and *Magnadigita*. Copeia (2):383-387, June 14.

Wellman, J.
1963. A revision of snakes of the genus Conophis (Family Colubridae, from Middle America). Univ. Kansas Publ. Mus. Nat. Hist., 15: 251-295, October 4.

Transmitted July 7, 1964.

29-7864

(Continued from inside of front cover)

9. Variation in the muscles and nerves of the leg in two genera of grouse (Tympanuchus and Pedioecetes). By E. Bruce Holmes. Pp. 363-474, 20 figures. October 25, 1962.
10. A new genus of Pennsylvanian Fish (Crossopterygii, Coelacanthiformes) from Kansas. By Joan Echols. Pp. 475-501, 7 figures. October 25, 1963.
11. Observations on the Mississippi Kite in southwestern Kansas. By Henry S. Fitch. Pp. 503-519. October 25, 1963.
12. Jaw musculature of the Mourning and White-winged doves. By Robert L. Merz. Pp. 521-551, 22 figures. October 25, 1963.
13. Thoracic and coracoid arteries in two families of birds, Columbidae and Hirundinidae. By Marion Anne Jenkinson. Pp. 553-573, 7 figures. March 2, 1964.
14. The breeding birds of Kansas. By Richard F. Johnson. Pp. 575-655, 10 figures. May 18, 1964.
15. The adductor muscles of the jaw in some primitive reptiles. By Richard C. Fox. Pp. 657-680, 11 figures in text. May 18, 1964.

Index. Pp. 681-694.

Vol. 13. 1. Five natural hybrid combinations in minnows (Cyprinidae). By Frank B. Cross and W. L. Minckley. Pp. 1-18. June 1, 1960.
2. A distributional study of the amphibians of the Isthmus of Tehuantepec, México. By William E. Duellman. Pp. 19-72, plates 1-8, 3 figures in text. August 16, 1960. 50 cents.
3. A new subspecies of the slider turtle (Pseudemys scripta) from Coahuila, México. By John M. Legler. Pp. 73-84, plates 9-12, 3 figures in text. August 16, 1960.
*4. Autecology of the copperhead. By Henry S. Fitch. Pp. 85-288, plates 13-20, 26 figures in text. November 30, 1960.
5. Occurrence of the garter snake, Thamnophis sirtalis, in the Great Plains and Rocky Mountains. By Henry S. Fitch and T. Paul Maslin. Pp. 289-308, 4 figures in text. February 10, 1961.
6. Fishes of the Wakarusa river in Kansas. By James E. Deacon and Artie L. Metcalf. Pp. 309-322, 1 figure in text. February 10, 1961.
7. Geographic variation in the North American cyprinid fish, Hybopsis gracilis. By Leonard J. Olund and Frank B. Cross. Pp. 323-348, plates 21-24, 2 figures in text. February 10, 1961.
8. Descriptions of two species of frogs, genus Ptychohyla; studies of American hylid frogs, V. By William E. Duellman. Pp. 349-357, plate 25, 2 figures in text. April 27, 1961.
9. Fish populations, following a drought, in the Neosho and Marais des Cygnes rivers of Kansas. By James Everett Deacon. Pp. 359-427, plates 26-30, 3 figures. August 11, 1961. 75 cents.
10. Recent soft-shelled turtles of North America (family Trionychidae). By Robert G. Webb. Pp. 429-611, plates 31-54, 24 figures in text. February 16, 1962. $2.00.

Index. Pp. 613-624.

Vol. 14. 1. Neotropical bats from western México. By Sydney Anderson. Pp. 1-8. October 24, 1960.
2. Geographic variation in the harvest mouse. Reithrodontomys megalotis, on the central Great Plains and in adjacent regions. By J. Knox Jones, Jr., and B. Mursaloglu. Pp. 9-27, 1 figure in text. July 24, 1961.
3. Mammals of Mesa Verde National Park, Colorado. By Sydney Anderson. Pp. 29-67, plates 1 and 2, 3 figures in text. July 24, 1961.
4. A new subspecies of the black myotis (bat) from eastern Mexico. By E. Raymond Hall and Ticul Alvarez. Pp. 69-72, 1 figure in text. December 29, 1961.
5. North American yellow bats, "Dasypterus," and a list of the named kinds of the genus Lasiurus Gray. By E. Raymond Hall and J. Knox Jones, Jr. Pp. 73-98, 4 figures in text. December 29, 1961.
6. Natural history of the brush mouse (Peromyscus boylii) in Kansas with description of a new subspecies. By Charles A. Long. Pp. 99-111, 1 figure in text. December 29, 1961.
7. Taxonomic status of some mice of the Peromyscus boylii group in eastern Mexico, with description of a new subspecies. By Ticul Alvarez. Pp. 113-120, 1 figure in text. December 29, 1961.
8. A new subspecies of ground squirrel (Spermophilus spilosoma) from Tamaulipas, Mexico. By Ticul Alvarez. Pp. 121-124. March 7, 1962.
9. Taxonomic status of the free-tailed bat, Tadarida yucatanica Miller. By J. Knox Jones, Jr., and Ticul Alvarez. Pp. 125-133, 1 figure in text. March 7, 1962.
10. A new doglike carnivore, genus Cynaretus, from the Clarendonian Pliocene, of Texas. By E. Raymond Hall and Walter W. Dalquest. Pp. 135-138, 2 figures in text. April 30, 1962.
11. A new subspecies of wood rat (Neotoma) from northeastern Mexico. By Ticul Alvarez. Pp. 139-143, April 30, 1962.
12. Noteworthy mammals from Sinaloa, Mexico. By J. Knox Jones, Jr., Ticul Alvarez, and M. Raymond Lee. Pp. 145-159, 1 figure in text. May 18, 1962.

(Continued on outside of back cover)

(Continued from inside of back cover)

13. A new bat (Myotis) from Mexico. By E. Raymond Hall. Pp. 161-164, 1 figure in text. May 21, 1962.
14. The mammals of Veracruz. By E. Raymond Hall and Walter W. Dalquest. Pp. 165-362, 2 figures. May 20, 1963. $2.00.
15. The recent mammals of Tamaulipas, México. By Ticul Alvarez. Pp. 363-473, 5 figures in text. May 20, 1963. $1.00.
16. A new subspecies of the fruit-eating bat, Sturnira ludovici, from western Mexico. By J. Knox Jones, Jr., and Gary L. Phillips. Pp. 475-481, 1 figure in text. March 2, 1964.
17. Records of the fossil mammal Sinclairella, Family Apatemyidae, from the Chadronian and Orellan. By William C. Clemens. Pp. 483-491. 2 figures in text. March 2, 1964.

More numbers will appear in volume 14.

Vol. 15. 1. The amphibians and reptiles of Michoacán, México. By William E. Duellman. Pp. 1-148, plates 1-6, 11 figures in text. December 20, 1961. $1.50.
2. Some reptiles and amphibians from Korea. By Robert G. Webb, J. Knox Jones, Jr., and George W. Byers. Pp. 149-173. January 31, 1962.
3. A new species of frog (Genus Tomodactylus) from western México. By Robert G. Webb. Pp. 175-181, 1 figure in text. March 7, 1962.
4. Type specimens of amphibians and reptiles in the Museum of Natural History, the University of Kansas. By William E. Duellman and Barbara Berg. Pp. 183-204. October 26, 1962.
5. Amphibians and Reptiles of the Rainforests of Southern El Petén, Guatemala. By William E. Duellman. Pp. 205-249, plates 7-10, 6 figures in text. October 4, 1963.
6. A revision of snakes of the genus Conophis (Family Colubridae, from Middle America). By John Wellman. Pp. 251-295, 9 figures in text. October 4, 1963.
7. A review of the Middle American tree frogs of the genus Ptychohyla. By William E. Duellman. Pp. 297-349, plates 11-18, 7 figures in text. October 18, 1963. 50 cents.
8. Natural history of the racer Coluber constrictor. By Henry S. Fitch. Pp. 351-468, plates 19-22, 20 figures in text. December 30, 1963. $1.00.
9. A review of the frogs of the Hyla bistincta group. By William E. Duellman. Pp. 469-491, 4 figures in text. March 2, 1964.
10. An ecological study of the garter snake, Thamnophis sirtalis. By Henry S. Fitch. Pp. 493-564, plates 23-25, 14 figures in text. May 17, 1965.
11. Breeding cycle in the ground skink, Lygosoma laterale. By Henry S. Fitch and Harry W. Greene. Pp. 565-575, 3 figures in text. May 17, 1965.
12. Amphibians and reptiles from the Yucatan Peninsula, México. By William E. Duellman. Pp. 577-614, 1 figure in text. June 22, 1965.

More numbers will appear in volume 15.

Vol. 16. 1. Distribution and taxonomy of Mammals of Nebraska. By J. Knox Jones, Jr. Pp. 1-356, pls. 1-4, 82 figures in text. October 1, 1964. $3.50.
2. Synopsis of the lagomorphs and rodents of Korea. By J. Knox Jones, Jr. and David H. Johnson. Pp 354-407. February 12, 1965.
3. Mammals from Isla Cozumel, Mexico, with description of a new species of harvest mouse. By J. Knox Jones, Jr. and Timothy E. Lawlor. Pp. 409-419, 1 fig. April 13, 1965.

More numbers will appear in volume 16.

Vol. 17. 1. Localities of fossil vertebrates obtained from the Niobrara Formation (Cretaceous) of Kansas. By David Bardack. Pp. 1-14. January 22, 1965.

More numbers will appear in volume 17.

- NA- L[awrence]

University of Kansas Publications
Museum of Natural History

Volume 15, No. 13, pp. 615-625, pls. 26-28, 2 figs.
July 20, 1965

MUS. COM. ZOO
LIBRARY
DEC 31 1965
HARVARD
UNIVERSITY

A New Species of Turtle, Genus Kinosternon, From Central America

BY

JOHN M. LEGLER

University of Kansas
Lawrence
1965

University of Kansas Publications, Museum of Natural History
Editors: E. Raymond Hall, Chairman, Henry S. Fitch,
Frank B. Cross

Volume 15, No. 13, pp. 615-625
Published July 20, 1965

University of Kansas
Lawrence, Kansas

PRINTED BY
ROBERT R. (BOB) SANDERS, STATE PRINTER
TOPEKA, KANSAS
1965

30-5832

S - NA - L [aurence]

MUS. COM... LIBRARY
DEC 31 19..
HARVARD UNIVERSITY

A New Species of Turtle, Genus Kinosternon, From Central America

BY

JOHN M. LEGLER

In 1957 Dr. Edward H. Taylor asked me to study and report on a specimen of *Kinosternon*, obtained by him in Costa Rica, that differed from other known species. Description was delayed for want of comparative material. In the three years 1961-63 I collected, prepared, and studied some 700 specimens of the genus *Kinosternon* from Central America. Among these are 13 additional individuals of the species represented by Dr. Taylor's specimen. The species is named and described as follows:

Kinosternon angustipons new species

Holotype.—University of Kansas 43631, adult female, alcoholic; Los Diamantes, Limón Province, Costa Rica; obtained by Edward H. Taylor and John Baker, August 13, 1952; original number 8507.

Paratypes (total of 13).—University of Utah 3756♂, 13 mi. S. San Juan del Norte, Nicaragua *in* Limón Prov., Costa Rica; UU 3757-60,62-64, KU 84882♂♂, UU 3765-66♀♀, .6 mi. NNW Puerto Viejo, Heredia Prov., Costa Rica; UU 3767♀, 2 mi. E and 1¾ mi. S Guabito, Bocas del Toro Province, Panamá and, UU 4189♂, 2 mi. NW Almirante, Bocas del Toro Province, Panamá.

Diagnosis.—A small species of *Kinosternon*, most closely resembling *K. dunni* Schmidt (1947), and having: 1) a flattened, noncarinate carapace; 2) a narrow plastron with anal notch and interlaminal seams that tend to fill with soft tissue in older individuals; 3) a narrow bridge (20% or less of length of carapace); 4) an unstriped head; 5) a maxillary beak that is neither hooked nor notched; 6) clasping organs on posterior limbs of males; and, 7) tip of tail unmodified (neither horn-covered nor clawlike) in both sexes.

Description of species (based upon type series).—Carapace relatively low (highest point on posterior part of fourth central), evenly arched or flat-topped in cross section, oval in dorsal aspect, greatest width usually at level of bridge. No pronounced sculpturing, even in smallest individuals; faint suggestion (creases) of mid-dorsal and dorsolateral keels in small specimens; no trace of dorsal keels in older, larger specimens. Anterior margin of carapace smooth, slightly indented; posterior margin shallowly notched (between postcentrals).

Carapacal scutes imbricated (juxtaposed only in old, worn specimens); first or third central longest and broadest, fifth central shortest and narrowest; centrals 1 to 3 approximately as long as broad, 4th and 5th significantly broader than long. Precentral wedge-shaped, narrowed anteriorly, usually broader than long, shorter than seam between first and second marginals. First central in narrow contact (or not in contact) with M_2. Tenth marginal highest, sloping gradually up from point of contact with M_9, abruptly higher than postcentrals; other marginals flat-topped. Two parallel lateral ridges along margin of carapace, the lower ridge continuous with anterior and posterior free edges of carapace and passing approximately through centers of marginals 4 to 7, the upper ridge continuous with upper borders of marginal scutes and terminating on M_{10}; a distinct marginal bulge between mentioned lateral ridges.

Plastron narrow, its freely movable lobes incompletely closing orifices of shell (extent of closure approximately 55 per cent for anterior lobe, 50 per cent for posterior); bridge narrow (17 to 20 per cent of carapace length), imparting subcruciform appearance to plastra of largest males. Plastral lobes constitute, respectively, approximately 33, 29, and 38 per cent of plastral length; posterior lobe constricted at hinge and having wide, shallow anal notch (more pronounced in males than in females). Interlaminal seams (especially those over hinges and the interfemorals) of older individuals containing varying amounts of soft pale tissue. Axillary and inguinal scutes in contact on bridge (narrowly separated in one old male); axillary scute narrowly in contact with M_4 and M_6; inguinal scute in broad contact with M_6 and M_7 (forming narrow contact with M_8 in two specimens). Plastral scutes, in order of length—abdominal, anal, humeral, femoral, gular, pectoral.

Head slightly broadened; snout wide and blunt in dorsal aspect as well as profile; maxillary sheath flat or slightly concave in premaxillary region, *neither hooked nor notched.* Tip of mandibular sheath blunt. Inner crushing surfaces of jaws weakly developed and chiefly smooth. Tomial edges of both sheaths nearly straight in profile. Snout, in general, evenly tapered, lacking pinched appearance characteristic of most other species of *Kinosternon.* Top of head evenly rounded in anterior view, lacking raised brows. Mature males having bosslike enlargement of snout in prefrontal region. Dorsal head shield present but indistinct, blending gradually with softer skin in temporal region.

Internal choanae broadly oval (approximately twice as long as broad); choanal flaps bearing a single papilla on anterior half of flap; free edge of flap (when closed) longitudinally bisecting choanal opening and papilla extending up to one half of remaining distance from edge of flap to medial border of opening. External narial openings directed anteriorly, situated just below tip of snout, round in cross section; floor of each narial passage having distinct, blunt, longitudinal ridge or papilla (clearly visible as a bulge just inside opening and slightly lateral to midventral floor of passage).

A linear series (usually three to six) of small barbels on each side of throat from mandibular symphysis to end of hyoid bar (and following course of that element), concentrated chiefly in triangular area bounded by mandibular rami; usually two or three smaller barbels on or near midline just posterior to symphysis; gular barbels variable in size but never so large as in *K. leucostomum,* and never consisting of enlarged mental pair with smaller ones behind. Skin of neck studded with distinct papillae having rounded white tips; papillae arranged, more or less regularly, in 14 to 16 longitudinal rows. Papillae numerous and distinct also on posterior surfaces of limbs and on tail (especially in perianal region). Hands and feet fully webbed, free edges of webs strongly fimbriated; antebrachium having three falciform scales on anterior surface.

Discrete, apposed patches of specialized scales (clasping organs) well developed on posterior thighs and legs of males; individual scales in each patch spadelike (not "tuberculate," not pointed); spadelike scales angled dorsally at approximately 45 degrees.

Tail of mature males elongate (equal to or longer than posterior plastral lobe), heavy at base, prehensile, and having blunt unmodified tip (not horn-covered, not clawlike). Tail of females not or barely extending to posterior margin of carapace.

Coloration.—The following descriptions are based upon live adults, viewed in clear water with a beam of incandescent light. Colors of live specimens are not significantly different from those which have been fixed and preserved in ethyl alcohol (no formalin used).

In general the colors of both sexes are drab and neutral. Adjacent pale and dark colors are never sharply delimited but grade gradually into one another. The pale snout, pale upper eyelids, and dark eye stand out clearly in lateral or dorsolateral views of the head and an observer's attention is drawn to them at first glance. This is not so in *K. leucostomum* in which the upper eyelids are either not pale or are joined in a continuously pale or mottled field with the frontal region and snout.

Female (UU 3767)

Iris brown, flecked with golden yellow, the combination appearing to be uniform dark brown except in bright light. Soft skin around nostrils cream; upper eyelids grayish cream; horny sheaths of jaws yellowish cream, grading into pale brown, the darker color being near junction of skin with horn. Ground color of limbs, tail, and dorsal part of neck pale gray to brownish gray, slate in darkest areas. Inguinal pockets grayish cream. Ventral surface of neck (except for a small gray area in front of plastron) yellowish cream, suffused with pink on gular region; a short, dull brown, indistinct stripe extending from mandibular symphysis (not on horny sheath) onto gular region. Top of head dark neutral brown with slight purplish cast, head shield slightly darker than softer skin behind it; side of head tannish above, grading gradually into paler color of throat; palest area on side of head over tympanum, same color as horny sheaths; a few indistinct, irregular, pale brown marks on side of head, chiefly near corner of mouth, below tympanum, and between tympanum and orbit.

Plastron dark golden yellow; interlaminal seams narrowly edged with dark brown; soft skin of interlaminal seams (where present) gray, same color as limbs. Undersurfaces of marginals slightly darker than plastron, pale color extending up to lower of two lateral marginal ridges. Carapace dark brown, having indistinct paler brownish areas near centers of scutes.

Male (UU 3757)

Iris somewhat paler than in female, having a pale reddish cast but consisting of brown and golden flecks (iris not distinct from pupil except in bright light). Jaw sheaths having fine, vertical, pale brown stripes. Ground color of plastron pale neutral yellow, much paler than in female.

Osteology.—Of Central American kinosternids, the skeleton of *Kinosternon leucostomum* bears the closest resemblance to *K. angustipons.* The following description is based upon two complete adult skeletons (UU 3760♂, UU 3766♀) and an adult shell (UU 4189♂) of *angustipons;* where skeletal characteristics are regarded as differing significantly from those of eight adult specimens of *leucostomum* (4 males and 4 females), the characteristics of *leucostomum* are given in brackets. In general, no significant differences were observed in the appendicular skeletons of the two species.

Skull solidly built, greatest width 65 to 66 per cent of total length, height 71 to 73 per cent of width; supraoccipital process relatively short, eight per cent of total length of skull [13 to 17 per cent in *leucostomum*]. Orbit relatively small and nearly circular, having substantial overhang of bone above; vertical diameter as a percentage of least interorbital breadth, 56 (♂) to 62 (♀) [orbit larger, relatively higher due to deficiency in overhang of bone above, vertical diameter 58 to 83 per cent (♂♂) and 68 to 74 per cent (♀♀) of least interorbital breadth]. Snout tapering anteriorly from base of postorbital bar [from point above mid-orbit]; top of skull (anterior aspect) more or less evenly rounded [more nearly flat-topped], dorsal orbital rim not at all jutting or browlike in appearance [distinctly jutting and browlike, albeit smaller]. Stapediotemporal foramen indistinct [distinct]. Temporal arch weakly emarginate below; quadratojugal comprising nearly one-half of temporal arch, jugal excluded from upper free edge of arch [jugal entering upper free edge]; crushing surfaces of maxillae poorly defined, not concave, sloping dorsomedially, especially weak in premaxillary region [concave; inner border sharp, distinct and continuous across premaxillary region]; anteroventralmost part of vomer greatly expanded, this expansion, the vomeropremaxillary articulation, and incisive foramina visible in ventral exposure [not so expanded, and structures mentioned excluded from ventral view by posterior premaxillary ridge]; maxillae widely separated anteriorly [in contact or closely approximated]; maxillary beak weakly or not at all developed; ventral part of snout lacking indented or "pinched" appearance in ventral view; profile of maxillary cutting edge forming nearly straight line [beak well developed; snout bilaterally

indented, having "pinched" appearance; profile of maxillary cutting edge recurvate]. Angular and coronoid bones of mandible not or but scarcely visible in direct lateral view; angular separating surangular and prearticular ventrally.

Cervical vertebrae typically kinosternid, second opisthocoelous, third biconvex, and remaining five procoelous; of these, sixth and seventh doubled posteriorly, seventh and eighth doubled anteriorly.

Phalangeal formula 2-3-3-3-3 on hand and foot (this assumes that metatarsal V is combined with a tarsal to form a single "hooked" element).

Primary sacral ribs expanded nearly to width of ilial blade at sacroiliac joint, narrow at distal articulation; secondary sacral ribs not at all expanded.

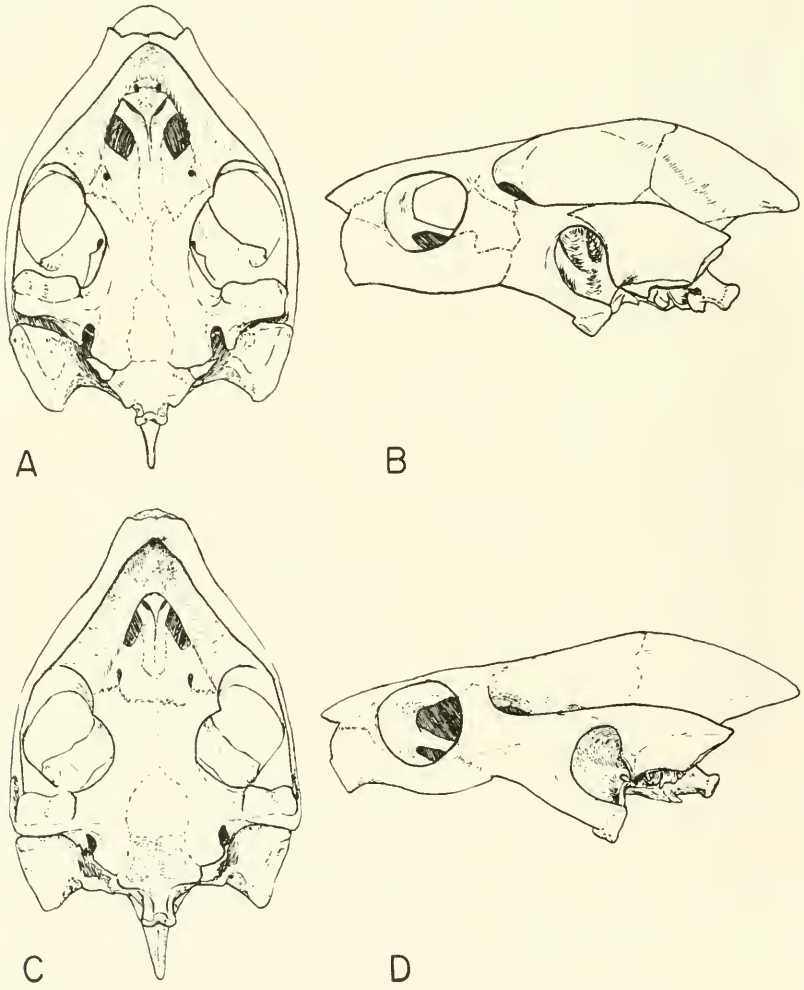
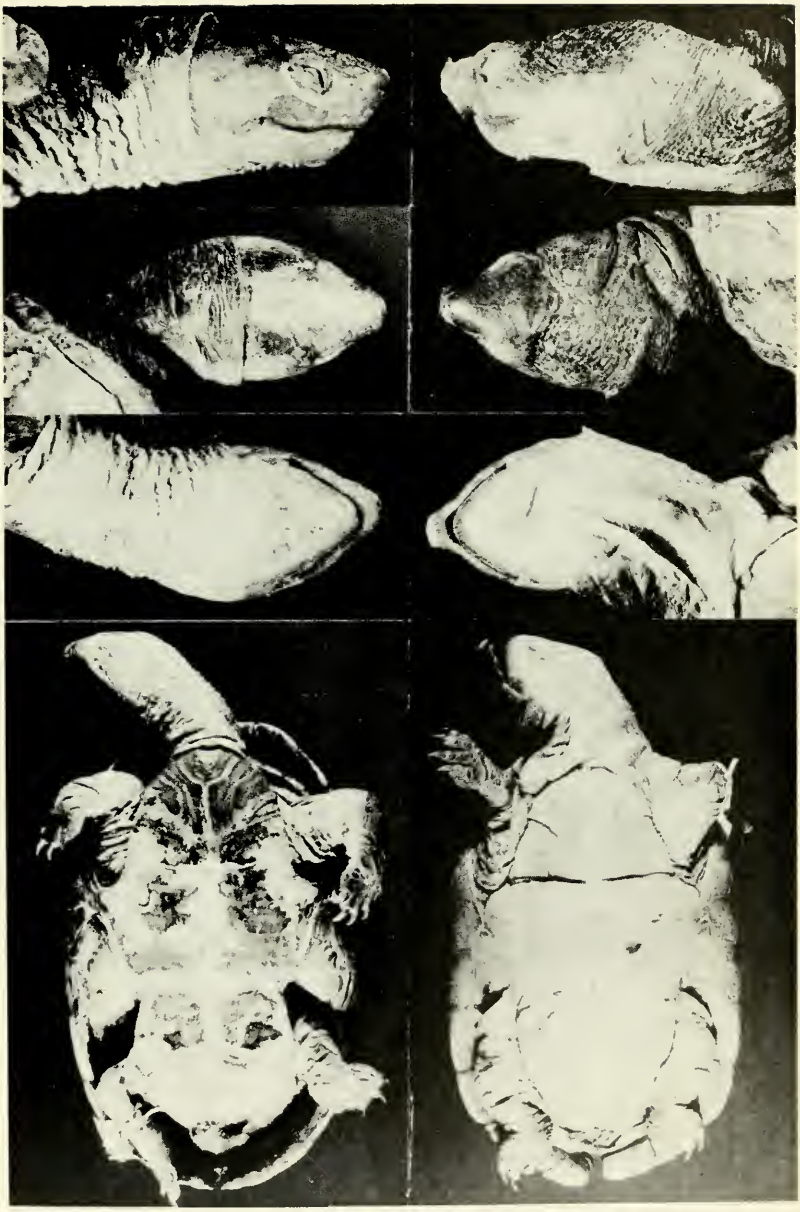
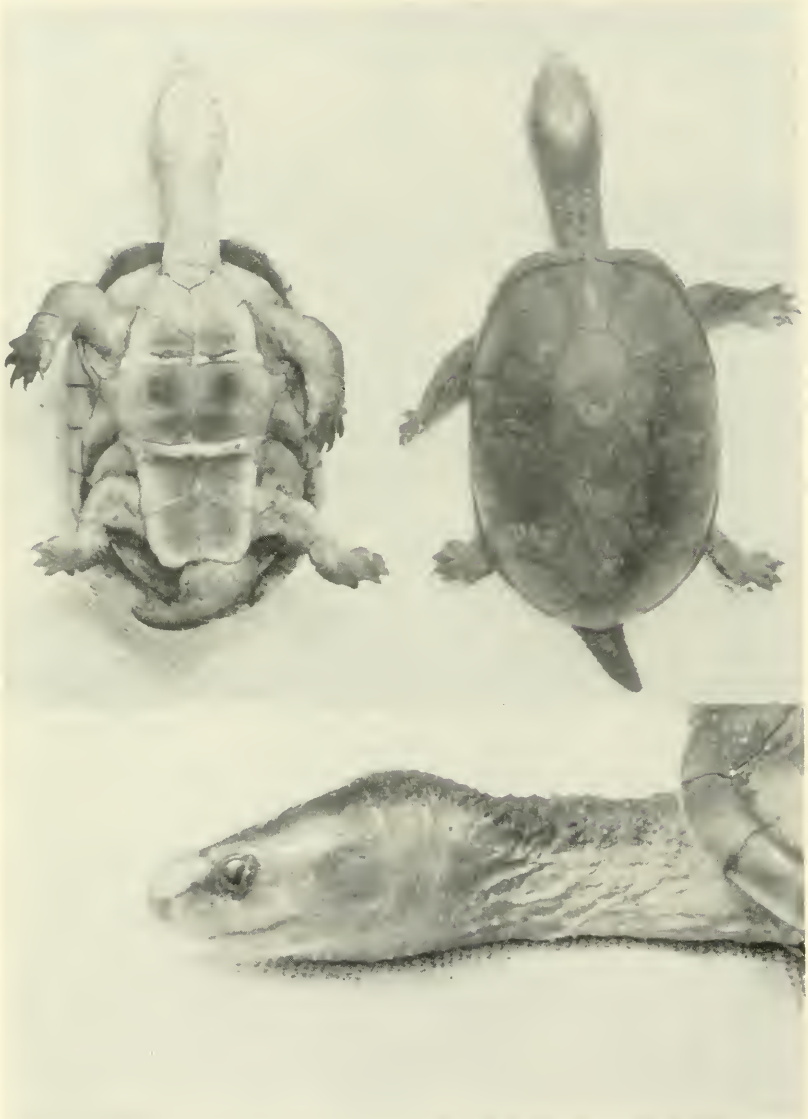


Fig. 1. A and B, Ventral and lateral views of skull, *Kinosternon angustipons*, paratype (UU 3766 ♀) × 2; C and D, skull of *K. leucostomum* (UU 4233 ♀, Gamboa, Canal Zone) × 2.

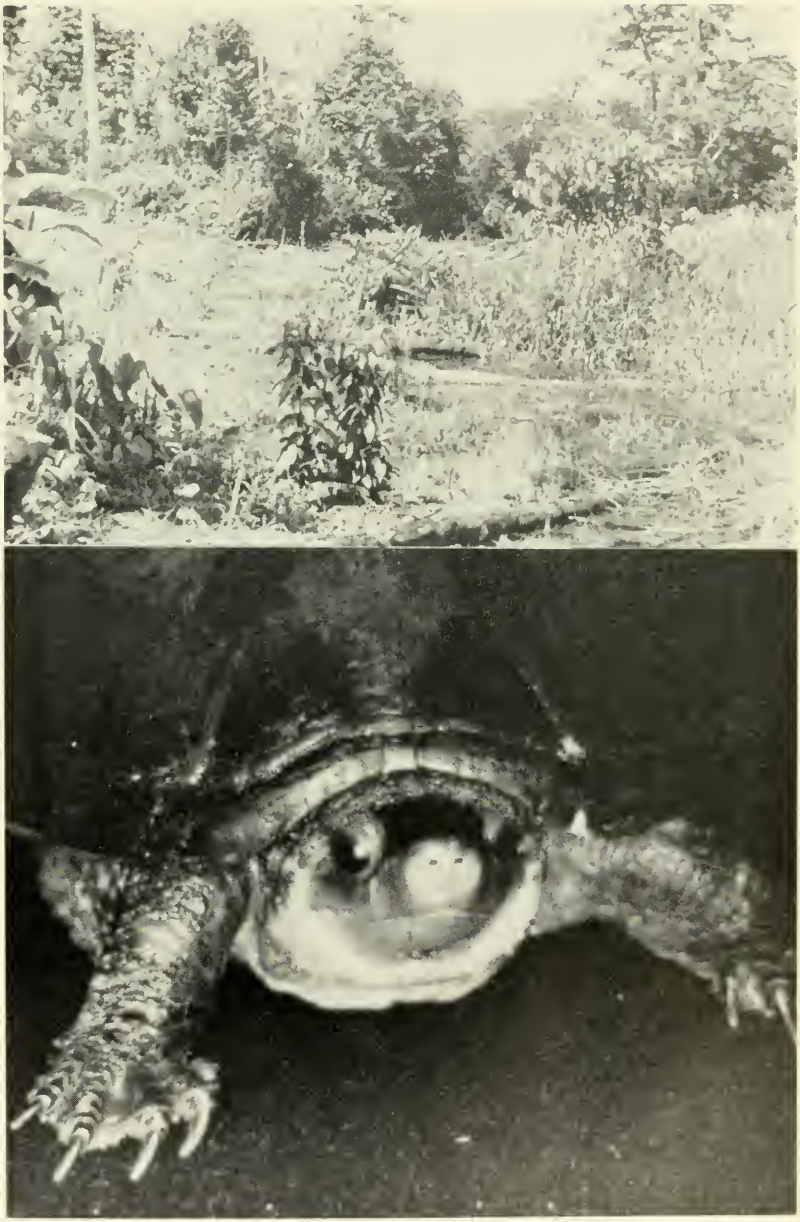
PLATE 26



Comparison of holotype, *Kinosternon angustipons* (left column) and paratype (CNHM 42803♀), *K. dunni* (right column); heads × .9; plastral views × .5 and .6, respectively.



Old male of *K. angustipons* (UU 3756), freshly killed; dorsal and ventral views × ½; head slightly larger than actual size; all photographs from color transparencies.



Top. Habitat of *K. angustipons*, .6 Mi. NNW Puerto Viejo, Heredia, Costa Rica, 22 July 1961. Nine specimens were obtained from small pool in foreground. *Bottom.* Anterior view of live female (UU 3767) showing pale snout and eyelids and unhooked beak, × 1½. All photographs from color transparencies.

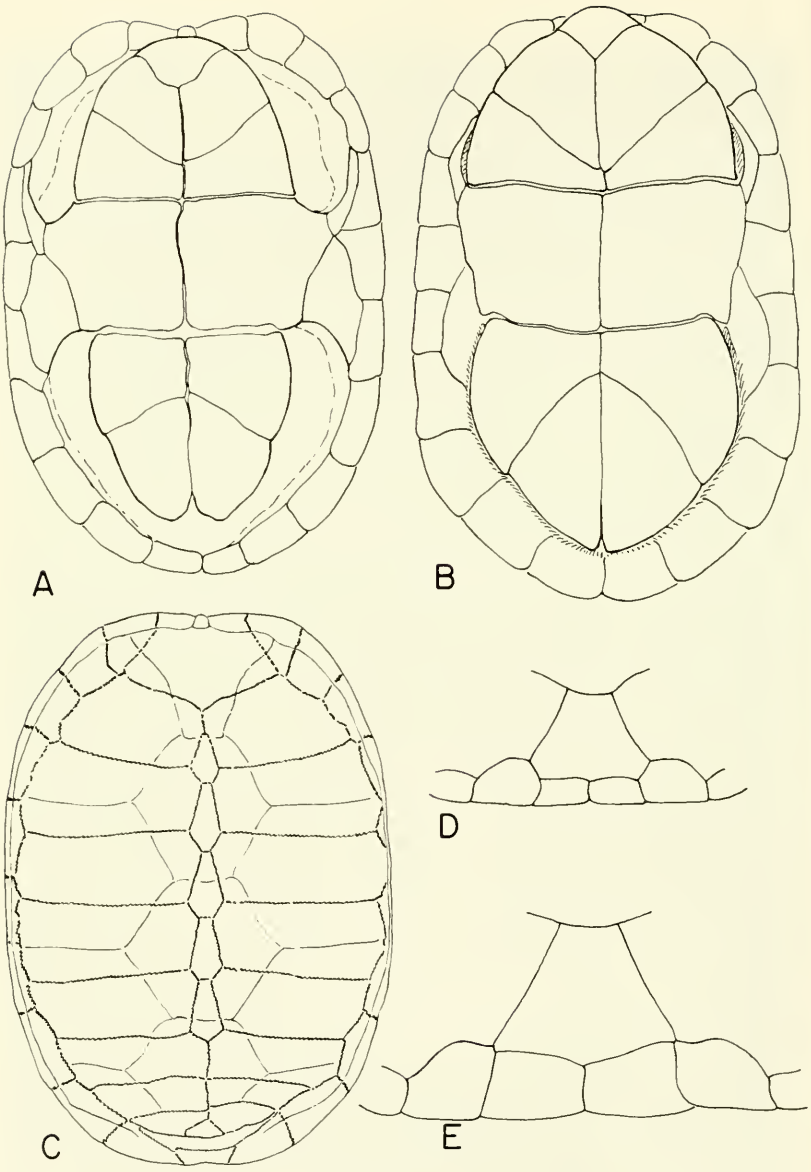


FIG. 2. A, Ventral view of shell, *Kinosternon angustipons*, paratype, (UU 3766♀) × .8; B, same view, *K. leucostomum* (UU 4232♂, Puerto Viejo, Heredia, Costa Rica) × .6; C, dorsal view of scuteless shell, *K. angustipons*, paratype (UU 3760♂) × .8; D and E, posterior margin of carapace showing fifth central lamina and the relative heights of postcentral and 10th marginal laminae in *K. angustipons* (UU 3766♀) and *K. leucostomum* (UU 4232♂), respectively (approximately × .85).

Caudal vertebrae 18 in ♂, 21 in ♀, distal two or three fused or nearly fused into blunt tip [terminal vertebrae fused into clawlike tip].

Five juxtaposed neurals, first neural separated from nuchal (by intercostal suture) by distance half its own length; shape of neurals basically hexagonal, long sides being anterior to an intercostal suture and short sides posterior in all specimens; pygal more or less rectangular, slightly notched; suprapygal six-sided, concave above, convex below, width approximately three times height [five-sided, width two times height]; small, subtriangular anterior suprapygal in two of three specimens [no anterior suprapygal]; of eight pairs of costals, last three pairs in mid-dorsal contact between last neural and anterior suprapygal, eighth pair only narrowly so [three, sometimes four pairs in *broad* contact]; first peripheral about as high as second, separated from its fellow (by nuchal) by width equal to or greater than its own; first peripheral in contact with first costal, separating nuchal and second peripheral [first peripheral much lower than second; nuchal and second in contact, excluding first peripheral from contact with first costal].

Comparison with other Central American species.—In my opinion there are four full species of *Kinosternon* in Central America south of the Republic of Mexico. These are *Kinosternon angustipons, K. acutum* Gray, *K. leucostomum* (including *K. postinguinal* Cope and *K. spurrelli* Boulenger), and *K. scorpioides* (Linnaeus) (including *K. panamensis* Schmidt and *K. cruentatum* Duméril, Bibron and Duméril). In *K. angustipons* the axillary scute is in narrow contact with the fourth marginal, never with the third; in the other three species the axillary is in contact with M_3 or narrowly separated from it, never separated by nearly the entire length of M_4. *K. angustipons* is further distinguished from these species in lacking a hooked, recurved maxillary beak and in lacking a distinct claw on the tip of the tail in both sexes. All these characteristics (except that of the maxillary beak) serve also to distinguish *K. dunni* from the other three species mentioned.

Comparison with Kinosternon dunni.—Differences in the heads and necks of the two species are the most striking, yet the most subjective (Pls. I-III). In profile *K. dunni* has a moderately hooked beak and recurved tomial edge on the maxillary sheath whereas *angustipons* has a flattened beak and a tomial edge that is nearly straight. In dorsal and ventral views the snout of *dunni* is much more pronounced, having a pinched appearance and probably being somewhat larger because of greater bulging of soft, circumnarial tissues. The snout of *angustipons* tapers evenly (unpinched) and is generally blunt in appearance. The dorsal head shield of *dunni* is sharply delimited whereas that of *angustipons* grades subtly into the softer skin of the neck.

The dermal papillae on the neck of *angustipons* are numerous, distinct, white-tipped, and arranged in regular longitudinal rows. There are also white-tipped papillae on the posterior surfaces of the limbs, the tail, and perianal region of *angustipons*. In *dunni* these dermal papillae are smaller, less numerous, less distinct, and irregularly arranged. Few papillae are discernible on the holotype (CNHM 42804) of *dunni* and those on the neck of the paratype (CNHM 42803) are restricted chiefly to a lateral row on each side. The tails and perianal regions of the two species are sharply differentiated, that of *angustipons* being distinctly papillose, and that of *dunni* being nearly bare.

Females of *angustipons* have relatively broad, short tails that are rounded (never pointed) and lack a terminal spine. Females of *dunni* have distinctly narrower tails, which are pointed. The holotype of *dunni* has a small terminal spine; the paratype does not.

On the holotype of *dunni* there is a deep distinct crease on each side of the middle plastral lobe (abdominal), beginning just behind the abdominal areola and extending to a point opposite the anterolateral corner of the posterior lobe. The middle lobe slopes angularly upward into the bridge lateral to the creases. The sides of the creases (especially the medial sides) form blunt, raised ridges. The creases are evident but weakly developed in the juvenal paratype of *dunni* and Medem's photographs (1961:465, fig. 8) indicate that at least the ridges are present on his specimens. No specimen of *K. angustipons* has such creases or ridges; the middle plastral lobe lies in approximately the same plane as the bridge or, if slightly lower, slopes into the bridge more gradually than in *dunni*. This feature of the plastron accounts, in part, for the relatively lower shell of *angustipons* (Table 1).

Consistent differences in shape of carapace are as follows: *dunni* tending to be widest at level of M_8, noticeably constricted opposite bridge (*angustipons* widest at point opposite bridge, not constricted, not flared posteriorly); large individuals of *dunni* having distinct, narrow, flattened area confined to central laminae, suggesting the weakly tricarinate condition found in some

TABLE 1. PROPORTIONAL DIFFERENCES BETWEEN *Kinosternon angustipons* SP. NOV. AND *K. dunni* SCHMIDT. DATA ARE BASED UPON 14 SPECIMENS OF *angustipons* (10♂♂ 4♀♀) AND UPON THE TYPES (EXAMINED) AND TWO OTHER SPECIMENS (NOT SEEN, MEDEM, 1961, 1962) OF *dunni* (1♂ 3♀♀). WHERE MEASUREMENTS OF *dunni* WERE NOT MADE FROM SPECIMENS, PROPORTIONS WERE COMPUTED FROM PUBLISHED DATA, DRAWINGS, OR PHOTOGRAPHS. STATEMENTS IN THE LEFT COLUMN REFER TO *angustipons*. ARITHMETIC MEAN, RANGE, AND STANDARD DEVIATION ARE GIVEN FOR EACH CHARACTER (SEPARATELY FOR EACH SEX IF CHARACTER JUDGED TO BE DIMORPHIC).

Condition in *K. angustipons*, and Character Measured	*K. angustipons*	*K. dunni*
Bridge relatively narrower; minimal width (anteroposterior) of bridge expressed as percentage of carapace length	18 ± 1.1 (17–20)	24 ± 0
Shell relatively lower; height of shell expressed as percentage of maximal width of carapace	♂♂ 55 ± 1.4 (51–56) ♀♀ 58 ± 3.6 (54–62)	♂ 65 ♀♀ 62 ± 3.16 (59–65)
Abdominal and anal scutes relatively shorter, pectoral and femoral scutes relatively longer; interlaminal length of each scute expressed as percentage of sum of median interlaminal lengths:		
Pectoral	8.3 ± 1.28 (6.8–10.8)	6.3 ± .97 (5.2–7.1)
Abdominal	29.8 ± 1.44 (26.7–31.7)	32.3 ± 2.27 (29.9–34.8)
Femoral	15.7 ± 1.88 (13.4–19.6)	11.7 ± 1.24 (10.3–12.5)
Anal	♂♂ 18.8 ± 2.21 (15.6–22.1) ♀♀ 22.8 ± 2.12 (19.6–23.9)	♂ 22.1 ♀♀ 25.7 ± .64 (25.2–26.1)
Head relatively narrower, especially in females; width of head expressed as percentage of carapace width	♂♂ 31 ± 1.5 (28–33) ♀♀ 29 ± 1.0 (28–30)	♂ 32 ♀♀ 35 ± 2.35 (31–35)
Plastron constricted at posterior hinge; width at hinge expressed as percentage of width (maximal) across femorals	94 ± 3.0 (90–102)	100 ± 1.6 (98–102)

populations of *K. scorpioides* (shell of *angustipons* more evenly rounded, not distinctly flat-topped in region of centrals).

Arithmetic expressions of these and other proportional differences between the two species are set forth in Table 1. The characters mentioned for the bridge, head, and posterior plastral hinge, however, are detectable without the aid of measurement and computation.

Size.—Use of adult size as a taxonomic character to compare small samples of turtles is hazardous; but, in some chelonians growth is determinate to the extent that: 1) it tapers off rapidly at a certain age or size and proceeds slowly or not apparently thereafter; 2) old individuals at or near maximum size are recognizable by external characteristics of the shell. It seems clear that the size attained by adults is at least partly under genetic control and that, if differences in size between two species can be demonstrated, they should be exploited as taxonomic characters.

The largest male of *angustipons* has a carapace length of 112 mm (nine other males range from 82 to 101) and the largest female a length of 119 (three others 90 to 109). Corresponding figures for known specimens of *dunni* are as follows: ♂ 171; ♀♀ 150, 149; a shell of unknown sex 175. The largest specimens of *angustipons* are clearly adults and, on the basis of appearance of shell, are past the age of normal regular growth; hence, they are near the maximum size that they would have attained. The second largest male (UU 3756, 101 mm) is likewise near maximum size. The paratype of *dunni* (CNHM 42803, ♀ 93 mm) is probably immature, whereas all females of *angustipons* are mature. I therefore regard the difference in adult size of *angustipons* and *dunni* as too great to be attributed to fortuitous sampling; *angustipons* is much the smaller of the two species and probably never attains the relatively ponderous bulk of *dunni*.

Localities and *Habitat.* Localities mentioned for the paratypes are reckoned, for clarity, in terms of airline miles from geographic points which appear on most maps. The locality for UU 3756 lies on the southern edge of a large island formed by the Bravo and Colorado channels of the Río San Juan at its delta, just west of the confluence of the Río Chirripó and the Colorado Channel. Actual place of collection was ¼ mile E of a farm referred to locally as "Valiente." Specimens from Bocas del Toro Province, Panamá, were taken along the railroad of the Chiriquí Land Company. The localities, as marked along the right of way, are: Mile 22½ (UU 3767) and Mile 2 (UU 4189), the "miles" being reckoned from the railroad shops in Almirante. Los Diamantes is a farm on the railroad, approximately two miles east of Guápiles.

All specimens were collected by means of baited hoopnets in shallow permanent swamps or slow, scummy backwaters of streams. Traps set nearby in clearer, flowing water yielded specimens of *K. leucostomum* but no *angustipons*.

Geographic range.—*K. angustipons* is now known only from the specimens herein reported; hence, the known range of the species extends, in the Atlantic lowlands, approximately from the delta of the Río San Juan (on the boundary between Nicaragua and Costa Rica) to Almirante, Bocas del Toro, Panamá. Most of the localities from which specimens are known are near sea level (less than 100 M); Los Diamantes is the highest, having an elevation of approximately 260 meters. Satisfactory microhabitats for the species probably exist, almost continuously, from northeastern Honduras to Colon, Panamá.

Discussion.—It is evident from the data presented that *K. dunni* and *K. angustipons* are closely related but taxonomically distinguish-

able. There is insufficient evidence at present to evaluate judiciously the standing of these taxa, in terms of species *vs.* subspecies. The apparent rarity of both taxa and general lack of field work in critical areas combine to make the problem an irresolvable one now. *K. angustipons* is here regarded as a full species because it is morphologically distinctive and is not known to interbreed with *K. dunni* nor other kinosternids.

The gap separating the known ranges of *dunni* and *angustipons* is at least 400 miles (from Almirante to the mouth of the Río Atrato) and includes the whole of the Isthmian region of Panamá. Possibly the gap is more apparent than real. Until better evidence is available, I predict (by inference from studies of other aquatic chelonians in Central America) that *dunni* and *angustipons* constitute an example of a pair of closely related species of recent origin whose ranges are separated narrowly in the Isthmian region of Panamá. The species *Geoemyda funerea* (Cope) and *G. punctularia* (Daudin) constitute another such pair in the same region whereas *Staurotypus triporcatus* (Wiegmann) and *S. salvini* Gray probably constitute a like example in northwestern Central America.

Relationships.—Except for its evident close relationship to *K. dunni,* the relationship of *K. angustipons* to other members of the genus is not clear. The combination of narrow plastron and narrow bridge is a striking feature and is seen also, to variable degrees, in *Kinosternon bauri* Garman, *K. herrerai* Stejneger, *K. hirtipes* Wagler, and *K. subrubrum* (Lacépède). My own studies of these species indicate that none of them is especially closely related to *angustipons* or *dunni,* in spite of the plastral similarity. Beyond this, I am unable to assess the relationships of *K. angustipons* at the moment.

Remarks.—*Kinosternon angustipons* is seemingly nowhere well known by natives. The species is not utilized for food (kinosternids rarely are) and, to my knowledge, it has not been given a common name even in local areas where many persons are familiar with turtles. In western Panamá and northern Costa Rica, *K. angustipons* and *K. leucostomum* are called "Galápago." Most persons who confused the two species in this manner were quick to see the differences I pointed out to them.

The specific name *angustipons* is from the Latin *angustus* (narrow) and *pons* (bridge) meaning narrow bridged.

Acknowledgments.—I am grateful to Dr. William E. Duellman (University of Kansas) and Dr. Robert F. Inger (Chicago Natural History Museum) for the loan of specimens. The authorities of the Gorgas Memorial Laboratory in

Panamá (especially Drs. C. F. Johnson, M. Hertig, G. B. Fairchild, and P. Galindo) did much to facilitate field work in that country as did Dr. Alvaro Wille (University of Costa Rica) in Costa Rica. Messrs. C. M. Keenan and E. Mendez have provided additional specimens from Panamá. Messrs. Lee Bell and Nowlan Dean rendered capable assistance in the field. Elizabeth Lane made the drawings of the skull. Research on which this account is based was supported by the Society of Sigma Xi (RESA Grant) and the University of Utah Research Committee in 1960, and thereafter by the National Science Foundation (Grant # B-10173).

In August of 1964, after the above account was in press, I discovered that Mr. Wilfred T. Neill had prepared a description of the species newly named in this paper. My thanks go to Mr. Neill for having withdrawn his manuscript when he learned of mine.

LITERATURE CITED

Medem, F.

1961. Contribuciones al conocimiento sobre la morfología, ecología y distribución geográfica de la tortuga *Kinosternon dunni* K. P. Schmidt. Novedades Colombianas, 1(6):446-476, 13 figs., 2 tables, 1 map, 1 September.

1962. La distribución geográfica y ecología de Los Crocodylia y Testudinata en el departamento del Chocó. Rev. Acad. Colombiana Ciéncias Exactas, Físicas y Nat., 11(44):279-303; 56 figs. (comprising 20 pls.), folding map, December.

Schmidt, K. P.

1947. A new kinosternid turtle from Colombia. Fieldiana Zoology, 31(13):109-112, fig. 14, 11 April.

Museum of Zoology, University of Utah, Salt Lake City, Utah. *Transmitted to editor January 21, 1964.*

□

30-5832

S - NA - Lawrence

MUS. COMP. ZOOL
LIBRARY
FEB 4 1966
HARVARD
UNIVERSITY

UNIVERSITY OF KANSAS PUBLICATIONS
MUSEUM OF NATURAL HISTORY

Volume 15, No. 14, pp. 627-709, pls. 29-36, 5 figs.

December 30, 1965

A Biogeographic Account Of the Herpetofauna of Michoacán, México

BY

WILLIAM E. DUELLMAN

UNIVERSITY OF KANSAS
LAWRENCE
1965

UNIVERSITY OF KANSAS PUBLICATIONS
MUSEUM OF NATURAL HISTORY

Institutional libraries interested in publications exchange may obtain this series by addressing the Exchange Librarian, University of Kansas Library, Lawrence, Kansas. Copies for individuals, persons working in a particular field of study, may be obtained by addressing instead the Museum of Natural History, University of Kansas, Lawrence, Kansas. When individuals request copies from the Museum, 25 cents should be included, for each 100 pages or part thereof, for the purpose of defraying the costs of wrapping and mailing. For certain longer papers an additional amount, indicated below, toward some of the costs of production, is to be included.

° An asterisk designates those numbers of which the Museum's supply is exhausted.

Vol. 1. Nos. 1-26 and index. Pp. 1-638, 1946-1950.

°Vol. 2. (Complete) Mammals of Washington. By Walter W. Dalquest. Pp. 1-444, 140 figures in text. April 9, 1948.

Vol. 3. °1. The avifauna of Micronesia, its origin, evolution, and distribution. By Rollin H. Baker. Pp. 1-359, 16 figures in text. June 12, 1951.
°2. A quantitative study of the nocturnal migration of birds. By George H. Lowery, Jr. Pp. 361-472, 47 figures in text. June 29, 1951.
3. Phylogeny of the waxwings and allied birds. By M. Dale Arvey. Pp. 473-530, 49 figures in text, 13 tables. October 10, 1951.
°4. Birds from the state of Veracruz, Mexico. By George H. Lowery, Jr., and Walter W. Dalquest. Pp. 531-649, 7 figures in text, 2 tables. October 10, 1951.
Index. Pp. 651-681.

°Vol. 4. (Complete) American weasels. By E. Raymond Hall. Pp. 1-466, 41 plates, 31 figures in text. December 27, 1951.

Vol. 5. Nos. 1-37 and index. Pp. 1-676, 1951-1953.

°Vol. 6. (Complete) Mammals of Utah, *taxonomy and distribution*. By Stephen D. Durrant. Pp. 1-549, 91 figures in text, 30 tables. August 10, 1952.

Vol. 7. Nos. 1-15 and index. Pp. 1-651, 1952-1955.

Vol. 8. Nos. 1-10 and index. Pp. 1-675, 1954-1956.

Vol. 9. Nos. 1-23 and index. Pp. 1-690, 1955-1960.

Vol. 10. Nos. 1-10 and index. Pp. 1-626, 1956-1960.

Vol. 11. Nos. 1-10 and index. Pp. 1-703, 1958-1960.

Vol. 12. °1. Functional morphology of three bats: Eumops, Myotis, Macrotus. By Terry A. Vaughan. Pp. 1-153, 4 plates, 24 figures in text. July 8, 1959.
°2. The ancestry of modern Amphibia: a review of the evidence. By Theodore H. Eaton, Jr. Pp. 155-180, 10 figures in text. July 10, 1959.
3. The baculum in microtine rodents. By Sydney Anderson. Pp. 181-216, 49 figures in text. February 19, 1960.
°4. A new order of fishlike Amphibia from the Pennsylvanian of Kansas. By Theodore H. Eaton, Jr., and Peggy Lou Stewart. Pp. 217-240, 12 figures in text. May 2, 1960.
5. Natural history of the Bell Vireo, Vireo bellii Audubon. By Jon C. Barlow. Pp. 241-296, 6 figures in text. March 7, 1962.
6. Two new pelycosaurs from the lower Permian of Oklahoma. By Richard C. Fox. Pp. 297-307, 6 figures in text. May 21, 1962.
7. Vertebrates from the barrier island of Tamaulipas, México. By Robert K. Selander, Richard F. Johnston, B. J. Wilks, and Gerald G. Raun. Pp. 309-345, pls. 5-8. June 18, 1962.
8. Teeth of edestid sharks. By Theodore H. Eaton, Jr. Pp. 347-362, 10 figures in text. October 1, 1962.
9. Variation in the muscles and nerves of the leg in two genera of grouse (Tympanuchus and Pedioecetes). By E. Bruce Holmes. Pp. 363-474, 20 figures in text. October 25, 1963. $1.00.
10. A new genus of Pennsylvanian fish (Crossopterygii, Coelacanthiformes) from Kansas. By Joan Echols. Pp. 475-501, 7 figures in text. October 25, 1963.
11. Observations on the Mississippi kite in southwestern Kansas. By Henry S. Fitch. Pp. 503-519. October 25, 1963.
12. Jaw musculature of the Mourning and White-winged doves. By Robert L. Merz. Pp. 521-551, 22 figures in text. October 25, 1963.
13. Thoracic and coracoid arteries in two families of birds, Columbidae and Hirundinidae. By Marion Anne Jenkinson. Pp. 553-573, 7 figures in text. March 2, 1964.
14. The breeding birds of Kansas. By Richard F. Johnston. Pp. 575-655, 10 figures in text. May 18, 1964. 75 cents.
15. The adductor muscles of the jaw in some primitive reptiles. By Richard C. Fox. Pp. 657-680, 11 figures in text. May 18, 1964.
Index. Pp. 681-694.

(Continued on inside of back cover)

University of Kansas Publications
Museum of Natural History

Volume 15, No. 14, pp. 627-709, pls. 29-36, 5 figs.
December 30, 1965

A Biogeographic Account Of the Herpetofauna of Michoacán, México

BY

WILLIAM E. DUELLMAN

University of Kansas
Lawrence
1965

S - NA. 2 [illegible]

University of Kansas Publications, Museum of Natural History
Editors: E. Raymond Hall, Chairman, Henry S. Fitch,
Frank B. Cross

Volume 15, No. 14, pp. 627-709, pls. 29-36, 5 figs.
Published December 30, 1965

MUS. COMP. ZOOL
LIBRARY
FEB 4 19[illegible]
HARVARD
UNIVERSITY

University of Kansas
Lawrence, Kansas

PRINTED BY
ROBERT R. (BOB) SANDERS, STATE PRINTER
TOPEKA, KANSAS
1965
30-8425

A Biogeographic Account Of the Herpetofauna of Michoacán, México

BY

WILLIAM E. DUELLMAN

CONTENTS

PAGE

Introduction 629
Acknowledgments 631
Description of the Area 631
Physiography and Geology 632
Hydrography 635
Geological History 636
Climate 637
Vegetation 639
Composition of the Herpetofauna 650
Ecology of the Herpetofauna 650
Distribution Within Habitats 651
Altitudinal Distribution 659
Factors Affecting Distribution 662
Influence of Man 669
Analysis of Ecological Distribution 670
Geography of the Herpetofauna 673
Methods of Zoogeographic Analysis 673
Distribution of the Herpetofauna 677
Patterns of Distribution 687
Origin of the Herpetofauna 691
Origin of Present Patterns of Distribution 695
Pleistocene Biogeography 695
Dispersal Routes in Southwestern México 698
Speciation in Southwestern México 700
Summary 702
Literature Cited 704

INTRODUCTION

In a previous paper (Duellman, 1961) I presented a systematic account of the amphibians and reptiles of Michoacá; at that time I noted that a report on the biogeography of the herpetofauna was in

preparation. The following is the faunal analysis anticipated at that time.

The biogeographical synthesis presented here is, for the most part, based on data obtained in about twelve months of field work in Michoacán from 1951 to 1960 and on data obtained from the examination of 9676 specimens from Michoacán and countless individuals from other regions. I have utilized all kinds of biogeographic evidence from various sources and have drawn freely on literature pertaining to Michoacán and on any other sources that offered substantial evidence and ideas. All species of amphibians and reptiles that occur in Michoacán have been included in this synthesis, not only as they occur in Michoacán, but from beyond the limits of the state. Also, species that inhabit areas adjacent to Michoacán but that do not occur in that state have been included. Consequently, most of the species of amphibians and reptiles that inhabit southwestern México have been taken into consideration. Even so, the present work is definitive only for the herpetofauna of Michoacán. I hope that this work can be utilized as a basis for comparative faunal syntheses of adjacent regions in southwestern México.

In the preparation of this report I have given considerable thought to various zoogeographic principles and to methods of zoogeographic analysis. I have taken the opportunity to discuss various methods and their applicability to the herpetofauna of Michoacán. The result is a modified system of faunal analysis, proposed in the section on the geography of the herpetofauna. Hopefully, this system will be applicable to various groups of animals in other regions. Since 1931 herpetologists have been following Dunn's historical classification of the American herpetofaunas. On the basis of new historical evidence and modern ideas of phylogeny within the amphibians and reptiles I propose some modifications of Dunn's classification.

A comment is needed regarding terminology. Throughout this report I use the term "herpetofauna" to mean the total aggregate of species of amphibians and reptiles in a given region, without regard to ecological communities or historical origins. This term has been in use for many years; I think it is more meaningful than the terms "herpetogeny, herpetozoa, and herptiles." Many writers have used the terms "faunal assemblage" and "faunal element" synonymously. For the sake of convenience, I have used "faunal assemblage" to mean a geographic or ecological division of the herpetofauna, and I have used the term "faunal element" to mean a group of species

having the same geographic history, without regard to present assemblages. The ecological terminology used here is that of Kendeigh (1961).

In order to be consistent and avoid confusing non-taxonomists, I have used here the same names for taxa that were used in the systematic account (Duellman, 1961), even though some taxonomic changes have been proposed since that date. In the list below the names given in the left hand column are those used by Duellman (1961) and the names given in the right hand column are those names currently in use.

Bufo compactilis compactilis=Bufo compactilis
Hyla baudini=Smilisca baudini
Phyllodactylus homolepidurus=Phyllodactylus davisi
Phyllodactylus lanei=Phyllodactylus lanei rupinus
Cnemidophorus scalaris=Cnemidophorus scalaris scalaris
Conophis vittatus vittatus=Conophis vittatus

Acknowledgments

Since the synthesis presented here is based on my previous work on Michoacán, all persons listed in the acknowledgments in that paper were in some way helpful in the accumulation of the data used here. I am especially grateful to Donald D. Brand of the University of Texas for his advice and helpful criticism of parts of the manuscript. Rogers McVaugh of the University of Michigan Herbarium patiently spent many hours helping me with botanical data and literature. Also, I am indebted to him for critically reading the section on vegetation. Much of the work on this report was done while I was associated with the Museum of Zoology at the University of Michigan. There and at the University of Kansas I profited from many discussions on Mexican biogeography with numerous colleagues. Which of the ideas presented here are theirs and which are mine I can no longer say, but I claim full responsibility for the statements in the following pages. Lastly, I thank Ann S. Duellman who aided me in gathering data, discussed with me many of the ideas presented here, and critically read the manuscript.

I respectfully dedicate this work to the memory of Professor Norman E. Hartweg, who fostered my early ambitions in Neotropical herpetology, offered guidance to this neophyte, and set an example of scholarly endeavor; were it not for him, this work might never have been initiated, let alone brought to completion. I only hope that he would have been pleased with the results.

DESCRIPTION OF THE AREA

The state of Michoacán comprises an area of 60,093 square kilometers (Vivo, 1958), lies between 17° 54′ and 20° 13′ North Latitude and 100° 02′ and 103° 47′ West Longitude, and borders on the Pacific Ocean for a distance of about 200 airline kilometers. The rugged terrain has a total relief of nearly 4000 meters.

Physiography and Geology

If a person were to view Michoacán from an altitude of several thousand meters at a point off the coast of southwestern México, he would see in some places a narrow coastal plain with mountains rising to an elevation of about 3000 meters, then an abrupt drop into a low broad valley followed by a chain of volcanoes, some of which rise to elevations of nearly 4000 meters. Beyond these volcanoes at a somewhat lower elevation he would see a plateau, the rolling terrain of which is frequently broken by small mountain ranges and lakes. My purpose here is to correlate the physiographic features of Michoacán with those of all southwestern México, especially those thought to be important in interpreting the distribution of the herpetofauna in the region.

Thayer (1916) outlined the physiographic regions of México. His work subsequently was modified by other geographers, such as Ordoñez (1941), Tamayo (1941), and Robles (1942). Although the terminology of the provinces differs in these works, the general conclusions of each are the same. Tamayo (1949) summarized the earlier work and presented a synthesis of Mexican physiography. The following classification of the physiographic provinces of Michoacán and surrounding area is only slightly modified from the synthesis given by Tamayo; the Spanish names for the provinces (if different) are given in parentheses (Fig. 1).

Lowlands.—

Pacific Coastal Plain (Planicie Costera del Pacífico)

Balsas-Tepalcatepec Basin (Depresión del Balsas)

Highlands.—

Mexican Plateau (Mesa Central or Altiplanicie Mexicana)

Cordillera Volcánica

Sierra de Coalcomán

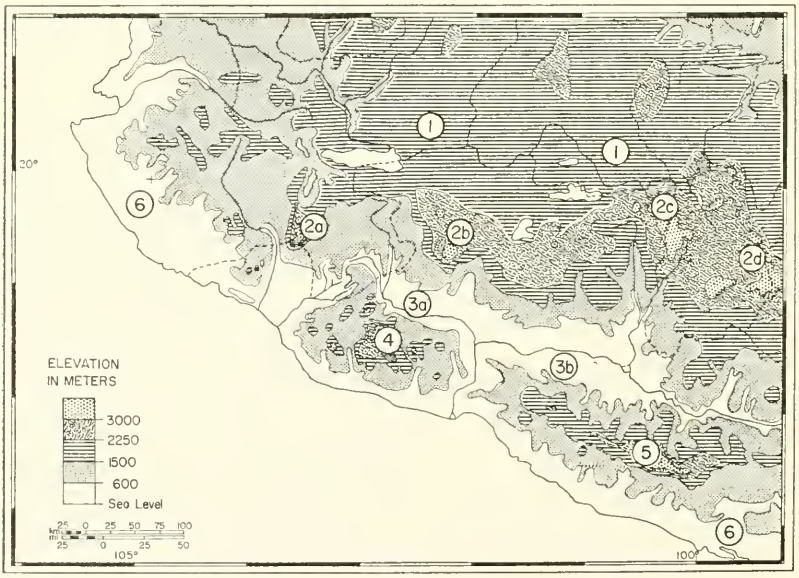


Fig. 1. Physiographic map of southwestern México.

The coastal region of Michoacán has been studied in detail by Brand (1957, 1958); most of the information presented here is a summary of his extensive reports. Although some areas seem to have had a recent history of submergence, most tof the coast seems to be rising. Only in the northwestern and southeastern coastal areas in Michoacán does an actual coastal plain exist. The plain is broad at the Río Coahuayana (the boundary between Colima and Michoacán); from this point the plain becomes narrower until Punta San Juan de Lima is reached about 10 kilometers airline from the mouth of the Río Coahuayana (Boca de Apiza). From Punta San Juan de Lima to Las Peñas (about 150 kilometers airline) the coast consists of rocky promontories and sea cliffs separated by sandy or shingle beaches (Pl. 1, fig. 1). Some of the promontories, such as Punta San Juan de Lima, rise abruptly from the sea to elevations of more than 200 meters. Many of the beaches are short and crescent-shaped; others are five to eight kilometers long. From Las Peñas to the delta of the Río Balsas, a distance of about 30 kilometers, there is a coastal plain; this is broadest near the Río Balsas, where the hills rise some 12 kilometers inland from the sea. Small lagoons are found in areas where a coastal plain exists. Some of the promontories are composed of limestone. Others are composed of granites, andesites, and diorites; these are a part of an intrusive mass underlying the limestone of the Sierra de Coalcomán and coming to the surface in places as far as 20 kilometers inland. Some of the beaches are composed entirely of sand; others are composed of a mixture of sand and rock, whereas still others are rocky (shingle beaches). According to Swadley (1958), the beach sands are predominately of igneous and metamorphic sources, with minor traces of volcanic sands. His analysis of beach sands indicates a southeast long-shore current.

Lying north of the Sierra de Coalcomán and the Sierra del Sur and south of the Cordillera Volcánica, and extending WNW-ESE is a broad structural depression, the Balsas-Tepalcatepec Basin. The western part, beginning in southern Jalisco and about 130 kilometers in length, is occupied by the Río Tepalcatepec, a major tributary of the Río Balsas, which occupies the eastern part of the depression. From the point of junction of the Río Tepalcatepec with the Río Balsas, the basin extends eastward for about 400 kilometers, terminating in southwestern Puebla and northwestern Oaxaca. In Michoacán the floor of the valley varies from 200 to about 700 meters above sea level. The terrain is relatively flat or rolling, frequently interrupted by barrancas formed by the many tributaries of the major rivers. The Río Tepalcatepec closely follows the front of the Sierra de Coalcomán, which rises abruptly from the floor of the valley (Pl. 1, fig. 2). The scarp on the north side of the basin is more gentle; its original nature has been obscured by extensive volcanism and erosion. Apparently the Tepalcatepec Valley and the lower east-west versant of the Balsas Valley represent a graben formed by faulting along what is now the northern scarp of the Sierra de Coalcomán and Sierra Madre del Sur, and a similar scarp on the north side of the basin. The presence of numerous hanging valleys in the north-central part of the Sierra de Coalcomán and in the Guerreran section of the Sierra Madre del Sur help substantiate this hypothesis. Seemingly the base rock of the depression is shale and sandstone; both are found as extensive exposures in the barrancas of the Río Marquéz and Río Cancita. Superimposed on the base rock is a variety of alluvium eroded from the surrounding mountains. Volcanic rocks are abundant, especially in the Tepalcatepec Valley. The headwaters of the Río Tepalcatepec

in southeastern Jalisco, especially the tributary, Río San Gerónimo, are only narrowly separated from the headwaters of the Río Ahuijullo, a tributary of the Río Coahuayana. Ridges less than 600 meters in elevation intervene between these river systems. The Ahuijullo depression presents a continuous lowland connection between the Tepalcatepec Valley and the lowlands of Colima; possibly in the past this depression was the drainage outlet of the present Balsas-Tepalcatepec Basin (see following section of the geological history). Shortly below the confluence with the Río Tepalcatepec, the Río Balsas flows in a southerly course through a narrow gorge separating the Sierra de Coalcomán from the Sierra Madre del Sur and emerges onto the coastal plain and flows into the Pacific Ocean (Pl. 2, fig. 1).

The Mexican Plateau, which comprises the central part of México, reaches its highest elevations in the south; in Michoacán the plateau varies from about 1500 to 1900 meters above sea level. It is bordered on the south by a chain of volcanoes making up the Cordillera Volcánica. Between the western extension of the main part of the Cordillera Volcánica (the Volcán and Nevado de Colima are outliers to the south) and the southern extension of the Sierra Madre Occidental into northern Jalisco the central tableland is not separated from the coastal lowlands and the upper Tepalcatepec Valley by high mountains; instead the plateau gradually breaks down into rolling hills descending into the lowlands. Apparently the chief base rock of the plateau is limestone; conglomerates, rhyolitic and andesitic volcanic rocks, and sandstones are superimposed on the base rock. Lacustrine deposits surround the large lakes indicating that these lakes once were more extensive than at present.

The nearly unbroken chain of volcanoes comprising the Cordillera Volcánica extends along the southern scarp of the Mexican Plateau from Jalisco to central Veracruz. These volcanoes, the highest in México, are on the southern edge of the plateau and lie roughly along the nineteenth parallel. They are Nevado de Colima (4300 m.), Nevado de Toluca (4560 m.), Popocatépetl (5400 m.), Ixtaccíhuatl (5150 m.), La Malinche (4460 m.), and Citlaltépetl (5600 m.), as well as the highest mountains in Michoacán: Cerro San Andrés (3930 m.) and Cerro de Tancítaro (3870 m.). The most recent cones are Volcán Jorullo, lying to the south of the Cordillera Volcánica and formed in 1759, and Volcán Parícutin, formed in 1943. Different parts of the Cordillera Volcánica are known by different names. The area between Cerro de Tancítaro and Pátzcuaro is called the Sierra de los Tarascos; the range immediately to the east of Morelia is called the Sierra de Ozumatlán; the area to the north and east of the Sierra de Ozumatlán and including the Cerro San Andrés is frequently referred to as the Serranía de Ucareo; the high range just east of Zitácuaro and extending along the western border of the state of México is called the Sierra de Temazcaltepec; the high volcanoes in the central part of the state of México, in the Distrito Federal, and in northern Morelos are referred to as the Sierra Ajusco. The rugged terrain of the Cordillera Volcánica is formed by hundreds of volcanic cones, especially in the Sierra de los Tarascos (Pl. 2, fig. 2). These mountains are invaded from the lowlands by numerous barrancas resulting from the headward erosion of many of the larger tributaries of the Río Balsas and Río Tepalcatepec. According to studies of the volcanoes of the Parícutin region by Williams (1950), some intrusive granitic rocks are present on the surface, but most of the rocks are extrusive andesites and basaltics. The soils are principally volcanic sands and ash.

Lying between the Río Tepalcatepec and the Pacific Ocean and extending from the Río Coahuayana and Río Ahuijullo on the west to the Río Balsas on the east is the Sierra de Coalcomán, a mountain mass some 200 kilometers in length and 80 kilometers in width. Apparently the highest mountain in this range is Cerro de Barolosa slightly more than 3000 meters above sea level. Structurally this range is part of the Sierra Madre del Sur Physiographic Province of Guerrero and Oaxaca (Tamayo, 1941, and Robles, 1942), but physiographically the Sierra de Coalcomán is isolated from the Sierra Madre del Sur by the low valley of the Río Balsas. The seaward base of the Sierra de Coalcomán is made up of intrusive granites. The remainder of the sierra is mostly limestone. The central part of the range is a karst terrain of sink holes, caves, underground rivers, and dogtooth limestone. For the most part, the seaward slopes of the Sierra de Coalcomán are well eroded by the numerous streams and rivers flowing into the Pacific Ocean. Contrariwise, the northern face of the sierra, at least in the central and highest part, is an escarpment dropping into the Tepalcatepec Valley. A few small streams flow through hanging valleys and cascade into the valley. The principal soils in the Sierra de Coalcomán are clays.

Hydrography

With the exception of the numerous coastal rivers, the drainage of Michoacán falls into two river systems, the Lerma-Santiago and the Balsas-Tepalcatepec. The Río Lerma forms most of the northern boundary of the state and flows into Lago de Chapala. The Río Duero in the extreme northwestern part of the state is the only important tributary of the Río Lerma in Michoacán; most of the other tributaries are intermittent streams. Lago de Chapala is drained by the Río Grande de Santiago which flows northwestward into the Pacific Ocean. Essentially all of the Cordillera Volcánica and most of the Mexican Plateau in Michoacán are drained by the Río Balsas and its principal tributary the Río Tepalcatepec. The major streams flowing southward from the Cordillera Volcánic into the Balsas-Tepalcatepec Basin are from west to east: Río Cancita, Río Cupatitzio (= Marquéz), Río Tacámbaro (= Turicato), Río Chinapa, Río Tuxpan, and Río Zitácuaro; the last three rivers flow into the Río Cutzamala, which in turn flows into the Río Balsas. No large streams flow northward from the Sierra de Coalcomán into the basin. As mentioned previously, after receiving the Río Tepalcatepec, the Río Balsas flows southward through a narrow gorge into the Pacific Ocean.

With the exception of the Río Coahuayana and the Río Balsas, which drain relatively little of the Coalcomán block, the major streams draining the Sierra de Coalcomán and flowing into the Pacific Ocean are from west to east: Río del Ticuiz, Río Ostula, Río Cachán, Río Tupitina, Río Nexpa, Río Mexcalhuacán, Río Chuta, and Río del Carrizal. All of these originate in the highlands and flow in a southerly course to the sea.

On the southern part of the Mexican Plateau are several lakes, the three largest of which in Michoacán are: Lago de Chapala in the northwestern part of the state and partly in Jalisco, Lago de Cuitzeo in the north-central part of the state and partly in Guanajuato, and Lago de Pátzcuaro at the edge of the Cordillera Volcánica (pl. 3, fig. 1). Other lakes in the state include Lago de Zirahuan at the edge of the Cordillera Volcánica and Lago de Camécuaro near Tangancícuaro. Although Lago de Cuitzeo has an extensive lakebed, in dry years only a small part of it contains water.

Geological History

The following is a brief summary of the historical events that have formed the present terrain of Michoacán and that are important in understanding the distribution of plants and animals in the region. During the Cretaceous the area that is now Michoacán may have been part of a seaway known as the Balsas Portal that connected the Pacific Ocean and the Atlantic Ocean in the region of the southern part of the Mexican Geosyncline (Schuchert, 1935, and Imlay, 1944). Coinciding with the Laramide Revolution at the end of the Cretaceous there was an uplift of the Mexican Plateau. Following this uplift was a period of peneplanation; a subsequent orogeny with uplift took place again in the Miocene and Pliocene and raised the Mexican Plateau to its present elevation. The development of the Cordillera Volcánica is correlated with the last period of orogeny. According to Flores (1946) and Blásquez and García (1946), the oldest volcanic rocks in the Cordillera Volcánica in eastern Michoacán are of Miocene age. Alfonso de la O. Carreño (1943) assigned the great cones of the cordillera, including Tancítaro, Nevado de Colima, Nevado de Toluca, Ixtaccíhuatl, and Citlaltépetl, to the Pliocene. Apparently the volcanism initiated in the Miocene has continued without notable interruption to the present time.

The Sierra Madre del Sur was elevated at the end of the Cretaceous; during the Miocene another period of orogeny took place accompanied by extrusive and intrusive activity; this was followed by a period of volcanism and elevation again in the late Pliocene and Pleistocene (Garfias and Chapin, 1949).

The historical geology of southern Michoacán has been summarized by Brand (1958:150-2):

"The major tectonic developments in the Coalcomán region seem to have been as follows. We start by assuming an old landmass (sometimes called by the uncouth name of Del Sur Borderland) on the seaward side of the present shore or overlapping slightly on the present land. In Paleozoic and Mesozoic times this borderland varied from a narrow band that completely separated the Pacific from the Atlantic, through a series of long islands, to a peninsula—so far as our southwest Mexico is concerned. This borderland may have provided a basement of pre-Cretaceous crystallines if we attribute to it some of the metamorphics which are found along the coast from Jalisco to Chiapas. In Guerrero, Oaxaca and Chiapas the Jurassic-Cretaceous formations lie discordantly upon a basal complex of metamorphics. At any rate, this borderland contributed to the Cretaceous deposits which (especially in the Middle Cretaceous) have a marine fauna with a marked inshore or littoral nature. In the late Cretaceous-Paleocene there was an extensive granitic intrusion, uplifting, folding, overthrusting, and faulting. Great sinkings took place parallel to the folds, both on the seaward and landward sides. By the end of the Eocene the Mexcala-Balsas-Tepalcatepec graben had been down faulted as well as the Manzanillo and Acapulco troughs. So far the nature and chronology of the tectonic activity seem to be fairly well indicated by evidence from various portions of the socalled Sierra Madre del Sur Province, along the coast from Cape Corrientes to the Isthmus of Tehuantepec.

"During the Tertiary there were two outstanding times of volcanic eruptions and extrusions along fault lines—during the Paleocene-Eocene and during the Miocene-Pliocene. Apparently only the earlier of these extrusive periods was important in the Coalcomán region. There followed widespread denudation and erosion which stripped off most of the Tertiary volcanic mantle as well as the Turonian sedimentaries, and developed a peneplain surface. The remnants of this peneplain are seen best in the accordant summits between the Ostula and Tupitina rivers and inland past Tehuantepec

and San José de la Montaña. Again there was uplift, accompanied by local intrusions that resulted in dikes that cut the granitics as well as the Cretaceous sedimentaries. As a result of this uplift much of the seaward slope of the Coalcomán region was dissected to a late youth stage.

"Towards the end of the Tertiary, during the Miocene and Pliocene when some other parts of Mexico were being mantled with extrusives, there was a sinking along the Pacific coast. María Madre Island in the Tres Marías, for example, shows Miocene and Pliocene deposits, and probably deposits of this time underlie the Pleistocene and Recent deposits along the costs of Jalisco and Colima and in the Balsas delta. It is possible that at this time a headward-eroding stream tapped a great lake occupying the Mexcala-Balsas-Tepalcatepec graben and formed the Balsas river. This great lake, which did not last long enough to leave much evidence, may have been draining earlier to the west via the Ahuijullo depression.

"More recently there was a down warping of the entire coastal section of Michoacán along a hinge line that can be traced some 15 or 20 miles inland from and parallel to the shore. This hinge line is marked by such items as rapids in the Cachán and Balsas rivers, seismic epicenters, some affluents that enter their streams at nearly right angles, and possibly one of the two hot springs in southwestern Michoacán. This down warping probably produced the drowned effect at Calestas de Campos and other spots on the Michoacán coast and probably also on the Costa Grande of Guerrero. Also this down warping increased the erosive action and the carrying capacity of the streams along the coast, which probably explains the pebble and boulder conglomerates in the Balsas delta and elsewhere.

"Today the southwest coast of Michoacán is characterized by little vulcanism, great earthquake activity, little or no coastal plain, and a positive or upward movement. The Coalcomán block especially typifies these characteristics. There are no recent volcanic cones or basaltic flows, and there are but two hot springs (at Cuchumala northeast of Coire, and the Aguas Calientes de Cuilala) and the warm mineralized spring at La Majahuita."

The historical events that seem to have had the greatest effect on the present distribution of the herpetofauna in southwestern Michoacán are, of course, the more recent ones. Among these are the more recent independent histories of the Cordillera Volcánica (characterized by extensive volcanism) and the Sierra de Coalcomán (without volcanism), the relatively late connection of the Balsas-Tepalcatepec Basin to the western lowlands via the Ahuijullo depression and only recent connection of this interior basin with the coastal lowlands of much of Michoacán. Climatic fluctuation during the Pleistocene no doubt was important in establishing many of the present patterns of distribution. The Pleistocene biogeography will be discussed in a subsequent section of this paper.

Climate

The great amount of physical relief in Michoacán not only produces considerable climatic variations, but delimits these variations along sharp boundaries. Temperature within the region depends primarily on altitude (the cooling effect of the onshore breezes along the coast being an exception), and precipitation depends on the prevailing winds and the terrain (Fig. 2).

An analysis of vertical temperature gradients in Michoacán indicates that on an average the mean annual temperature decreases slightly less than 1° C. per 200 meter increase in elevation. Adequate meteorological records are not available for coastal Michoacán, but records for Manzanillo, Colima, and La Unión, Guerrero, show that at Manzanillo the mean annual temperature is 26.1° C. with a range from the coolest month (March) to the warmest

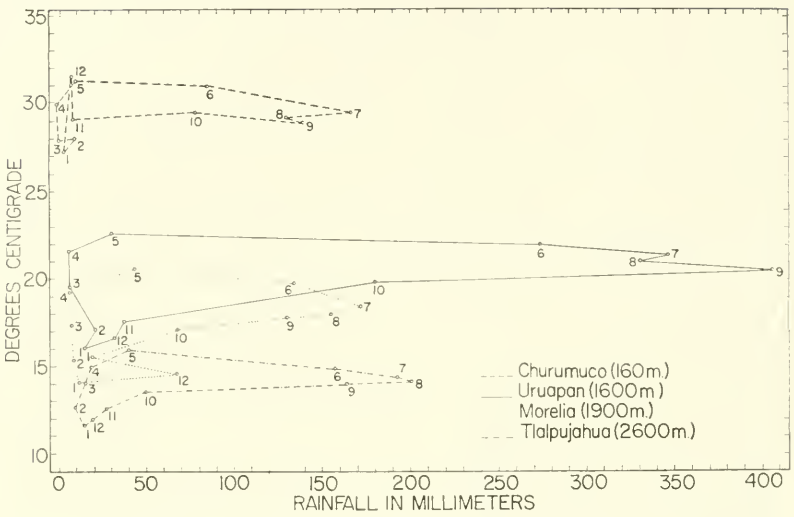


Fig. 2. Climatographs for four localities in different physiographic provinces in Michoacán.

month (July) of 4.6° C., and that at La Unión the mean annual temperature is 27.7° C. with a range from the coolest month (February) to the hottest month (June) of 2.5° C. (Contreras Arias, 1942). In the Balsas-Tepalcatepec Basin temperatures average higher than on the coast. At Churumuco the mean annual temperature is 29.3° C. with a range of monthly means of 3.5° C. The highest temperature recorded in the basin is 47.5° C. at Huetamo; temperatures at Apatzingán and Churumuco have exceeded 43° C. (Contreras Arias, 1942). Frosts and below freezing temperatures occur sporadically on the Mexican Plateau, where especially in winter the daily fluctuation in temperature can be of considerable magnitude. Temperatures below freezing have been recorded at Ciudad Hidalgo (elevation 2100 m.) for the months of October through March, and at Pátzcuaro (elevation 2200 m.) and Zacapu (elevation 2000 m.) for the months of November through March. In winter, snow falls on the higher mountains, especially Cerro de Barolosa, Cerro San Andrés, and Cerro de Tancítaro. Goldman (1951:189) stated:

"Our first sight of Cerro de Tancítaro from the summit of Cerro Patambán late in January was not long after a heavy storm, and the top of the northwest side was covered with snow down to about 11,000 feet near the lower border of the Hudsonian. At the time of our work on the mountain [February 20 to March 3, 1903], however, all this had gone except on the upper 500 or 600 feet, where from 1 to 2 feet of snow remained. The Indians living at the base of the mountain told us that snow sometimes covers the slopes down to about the 7,000 foot level."

The amount of precipitation in Michoacán varies geographically and seasonally. At least in the coastal region and in the Balsas-Tepalcatepec Basin, about 90 percent of the precipitation falls between the first of June and the end of October, with the highest rainfall in the month of September. According to Brand (1958:172):

"Northwest winds predominate along the Michoacán and Colima coast throughout most of the year. Next in frequency probably would come west-

erly and then northerly winds. These usually are of low or moderate force. However, in the June to September period, and often extending from May into October, there is a relatively high incidence of winds from the southerly quadrant (SE, S, SW). These southerly winds (and including winds from the west) are the principal ones that reach or exceed gale proportions."

Thus, at least in the rainy season, the prevailing winds blow directly off of the Pacific Ocean. This results in higher rainfall on the southern and western mountain slopes than on the northern and eastern slopes and definite rain shadows in the Balsas-Tepalcatepec Basin and on the Mexican Plateau immediately to the lee of the Cordillera Volcánica.

Inadequate records of rainfall are available for coastal Michoacán, for the only data are for three years at Coahuayana (average annual rainfall, 871 mm.). Manzanillo, Colima, has a mean annual rainfall of 1050 mm.; Tecomán, Colima, 786 mm.; La Unión, Guerrero, 1048 mm. Records for three stations in the Sierra de Coalcomán are: Aguililla, 986 mm.; Arteaga, 1125 mm.; and Coalcomán, 1179 mm. All three of these stations are situated in valleys of moderate elevation (800 to 1000 meters) and lie on the leeward sides of mountain ridges. The type of vegetation found between 150 and 600 meters on the windward (seaward) slopes of the Sierra de Coalcomán indicates that the precipitation in this zone is higher than on the coastal lowlands or in the higher mountains. Furthermore, the precipitation probably is more evenly distributed throughout the year, but still definitely seasonal. The highest annual rainfall in the state has been recorded at Uruapan (1683 mm.). From the nature of the vegetation I would expect a greater amount of rainfall on the windward slopes of the Sierra de Coalcomán.

The Balsas-Tepalcatepec Valley lies in a rain shadow created by the Sierra de Coalcomán and the Sierra Madre del Sur. In the valley the rainfall seldom exceeds 800 mm. per year. The months of January through April are exceedingly dry; sometimes no rain falls in this period. Likewise, on the Mexican Plateau there is little rainfall, usually not more than 1000 mm. per year, especially near the leeward base of the Cordillera Volcánica. Although records of rainfall are not available, the nature of the vegetation on the windward and leeward slopes of the Sierra de Coalcomán and the Cordillera Volcánica shows the effects of different amounts of precipitation. This is especially noticeable in the Sierra de Coalcomán, where at 500 meters on the windward slopes there is a relatively lush tall, broad-leaf forest, as contrasted with the scrubby thorn forest at the same elevation on the leeward slopes. In the high mountains the precipitation, although not great, is fairly well distributed throughout the year (see Tlalpujahua, fig. 2).

Vegetation

The previously described physiography, soils, and climate combine to produce a highly varied vegetation and diversified flora in Michoacán. The plant life ranges from tangled tropical "jungles" to thorny desert bushes and cacti; contrasting with these are the pine and fir forests on the mountain slopes. Neither a detailed description of the vegetation nor a relatively complete floral list for Michoacán is available at this time. Comprehensive studies of the vegetation of Pacific coastal states in México have been published only for the Río Mayo area in southern Sonora (Gentry, 1942) and for Chiapas (Miranda, 1952). Nevertheless, sufficient data have been compiled to permit a general discussion of the vegetation in Michoacán and a presentation of an

outline of animal habitats in the state similar to that prepared for Honduras by Carr (1950).

The following discussion is based on observations and collections made by me and my field associates, on a collection made by B. L. Turner in 1950 and identified by Rogers McVaugh of the University of Michigan Herbarium, on the botanical data given by Goldman (1951), and on the detailed account of the vegetation between Apatzingán and Cerro de Tancítaro presented by Leavenworth (1946). Also, I have benefited from information provided by Donald D. Brand and Rogers McVaugh.

One of the things most evident to the traveler in México is the great amount of land that has been cleared of its natural vegetation and that is being used for agricultural purposes, or has been so used. This is especially true for the southern part of the Mexican Plateau where Indians have cultivated the land for many centuries. In recent years the amount of arable land has been greatly increased through irrigation. Broad expanses of former mesquite-grassland in the northwestern part of Michoacán and in the upper valley of the Río Tuxpan are under irrigation. Irrigation has made possible varied agriculture in the arid Tepalcatepec Valley, where previously scrubby legumes and cacti were the conspicuous plants. On the Mexican Plateau maize and wheat are common crops; in the Tepalcatepec Valley melons, tomatoes, maize, sesame, rice, and citrus fruits are grown in abundance. On the coastal lowlands some land is used for subsistence agriculture and some for coconuts, bananas, cotton, and sesame. Other extensive areas are used for grazing.

Agricultural malpractices and heavy over-grazing probably are among the chief causes for development of the present cactus-thorn scrub associations on the Mexican Plateau in Michoacán and adjacent states. Much of the pine forest in the Sierra de los Tarascos is heavily grazed by goats, with the result that there is little undergrowth except closely cropped grass, and the forest presents a parklike appearance. Many forested areas have been at least partly cut by the omnipresent charcoal burners, who every day drive their heavily laden burros from the mountain forests to villages and towns. This age-old practice has resulted in the cutting of countless trees each year. Prehistoric Tarascan religion required perpetual fires and thus the consumption of great quantities of fuel. Now lumber companies have the timber rights to some of the remaining extensive forests of pine and oak.

The ravages by man during the past few centuries have made it difficult to determine the natural vegetation in many areas. With the increased use of irrigation and modern agricultural machinery far greater areas soon may be under cultivation, and with the application of modern lumbering methods the remaining areas of virgin forest may be cleared.

For the purposes of this account I have attempted to present a simplified classification of the major vegetation types in the state and to discuss these with respect to their distribution, physiognomy, and characteristic flora. The classification used here is a modified version of that proposed by Leopold (1950); the changes made by me reflect the attempt to present a classification of animal habitats based on vegetation type and not solely a classification of vegetation types.

The major vegetation types, and likewise animal habitats, can be divided into two groups with the subdivisions shown below (Fig. 3):

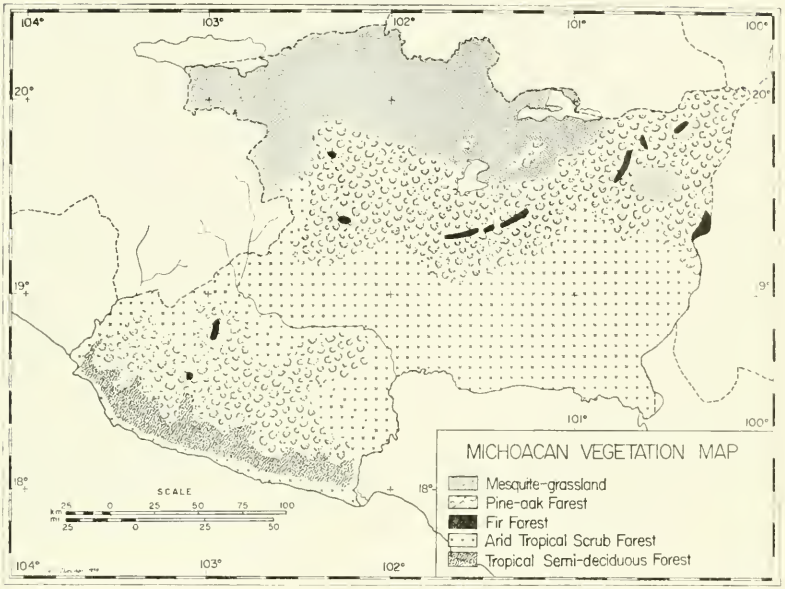


FIG. 3. Generalized vegetation map of Michoacán.

TEMPERATE (1000-4000 meters)
Fir Forest (2400-4000 meters)
Pine-Oak Forest (1000-4000 meters)
Mesquite-Grassland (1500-2100 meters)

TROPICAL (0-1000 meters)
Arid Tropical Scrub Forest (0-1000 meters)
Tropical Semi-Deciduous Forest (150-600 meters)

Pine-oak forest and mesquite grassland as used here are essentially the same as outlined by Leopold (1950); however, Leopold placed some pine and oak forests in the "Boreal Forest." I have separated the pine and oak forests entirely from the boreal element because of the distinctly different animal environment provided by the fir forest (boreal) and the pine and oak forests. Arid tropical scrub forest, as visualized here, is a combination of Leopold's arid tropical scrub forest and thorn forest. Similarities in the animal environments provided by the scrub forest on the coastal lowlands and that in the Tepalcatepec Valley overshadow minor differences in structure and floral composition. I have refrained from separating the scrub forest in the Tepalcatepec Valley into subdivisions according to the density of the vegetation, as was done by Leavenworth (1946). Tropical semi-deciduous forest, as used here, is in part homologous with Leopold's "Tropical Deciduous Forest" and Gentry's (1942) "Short Tree Forest." At no time is the predominantly broad-leafed tall forest on the seaward slopes of the Sierra de Coalcomán completely deciduous; in the dry season the shade provided by the greenery of this forest is in marked contrast to the barren, nearly leafless scrub forest of the coastal lowlands.

There have been several classifications of vegetation types proposed for either extensive or restricted areas in México. As pointed out by Martin (1958a), the recognition of homologous habitats cannot be ignored by zoologists. Various vegetation classifications, including those based on work in Nuevo León (Muller, 1939), the Río Mayo area in Sonora (Gentry, 1942), the Cerro de Tancítaro-Apatzingán transect (Leavenworth, 1946), Coahuila (Muller, 1947), all of México (Leopold, 1950), the state of Chiapas (Miranda, 1952) have been partly correlated by Martin (1958a) in his work on the Gómez Farías region in Tamaulipas. The above discussion of the differences between the classification presented here and that proposed by Leopold should suffice as a correlation between the present classification and those discussed by Martin.

In mountainous regions in the tropics, vegetation types are correlated with climate; this correlation in Nuevo León has been discussed by Muller (1939). The effects of altitude are reflected in the general distribution of the tropical and temperate environments in Michoacán; generally the temperate environments are above 1000 meters and the tropical ones below 1000 meters. The floral composition shows a similar correlation; the species making up the temperate vegetation in general have the centers of their distributions, or the centers of dispersal for their respective groups, to the north, whereas the opposite is true for most of the species in the tropical environments. With the exception of the cooling effect of the onshore breezes in the coastal lowlands, the temperature is closely correlated with altitude. Thus, the arid tropical scrub forest and tropical semi-deciduous forest are the hot environments; the lower pine-oak zone is somewhat cooler; the pine forests and mesquite-grasslands have moderate temperatures, and the high pine forests and fir forests are cool. Correlating rainfall and vegetation is more complicated. The mountainous terrain results in the formation of rainy zones on windward sides of mountains and rain shadows on the leeward sides of these mountains; for example, the Tepalcatepec Valley lies in a rain shadow on the leeward side of the Sierra de Coalcomán. In Michoacán the areas receiving the highest rainfall are the slopes of the Sierra de Coalcomán between 150 and 600 meters and the high ridges and peaks of the Sierra de Coalcomán and Cordillera Volcánica. On slopes of the Sierra de Coalcomán tropical semi-deciduous forest has developed, whereas on high ridges and peaks fir forest has developed. Thus, in Michoacán there is a hot and humid environment, the tropical semi-deciduous forest, and a cool and humid environment, the fir forest. Contrariwise, the arid tropical scrub forest is a hot and dry environment, and the mesquite-grassland is a temperate dry environment, having at least in the summer hot days and cool nights. Generally speaking, the pine-oak vegetation type, as discussed below, is a subhumid environment; however, where it exists on some of the higher ridges it is decidedly humid.

Before considering the major vegetation types as they occur in Michoacán, it is necessary to comment on certain types that do not occur there. Some writers, notably Storm (1939), suggest that tropical rainforest exists on the coast of Michoacán. I have found no evidence of rainforest in the state, nor do I know of its existence on the Pacific coast of México northwest of Chiapas. The dense tropical semi-deciduous forest sometimes encountered along permanent streams in the coastal barrancas probably is the basis for these reports [for a discussion of the supposed rainforest in Barranca de Bejuco, Michoacán,

FIG. 1. Promontories and beach immediately east of the mouth of the Río Tizupan, coast of Michoacán. July, 1951.

FIG. 2. North face of the Sierra de Coalcomán as seen from the Río Tepalcatepec, southeast of Apatzingán. June, 1955.

FIG. 1. Gorge of the Río Balsas separating the Sierra de Coalcomán (left) from the Sierra Madre del Sur (right). Aerial photograph by Donald D. Brand.

FIG. 2. Volcán Parícutin in the Sierra de los Tarascos, Cordillera Volcánica, Michoacán. Lava flows and remains of church in San Juan de Parangaricutiro are visible in middle. July, 1951.

FIG. 1. Southeastern shore of Lago de Chapala, just west of La Palma, Michoacán. June, 1955.

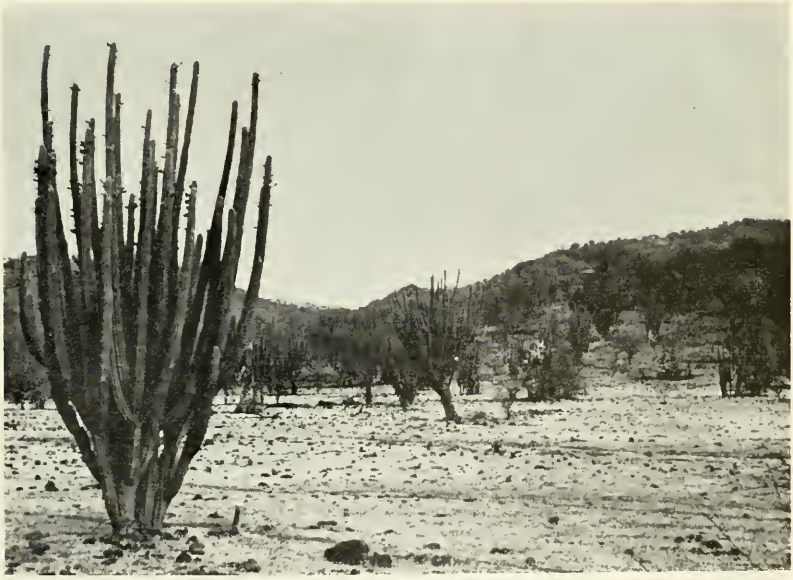


FIG. 2. Columnar cacti in arid tropical scrub forest in dry season at Zicuiran in the Tepalcatepec Valley. April, 1956.

FIG. 1. Open arid tropical scrub forest 4 kilometers north of Capirio, Michoacán. Photographed in rainy season, August, 1956.

FIG. 2. Trail entering tropical semi-deciduous forest at San Pedro Naranejstila, Michoacán. August, 1951.

FIG. 1. Gigantic parota tree (*Enterolobium cyclocarpum*) between Pómaro and Rancho El Diezmo, Michoacán. July, 1951.

FIG. 2. Relatively undisturbed mesquite-grassland near Zamora on the Mexican Plateau. Photograph by T. J. Cohn, September, 1958.

FIG. 1. *Opuntia-Acacia-Agave* association in mesquite-grassland at south edge of Lago de Cuitzeo, Michoacán. June, 1958.

FIG. 2. Open pine-oak forest near Rancho Los Pozos, Sierra de Coalcomán, Michoacán. July, 1951.

FIG. 1. Humid oak forest at Dos Aguas, Sierra de Coalcomán, Michoacán. Note abundant epiphytes. June, 1958.

FIG. 2. Oak forest at Cascada Tzararacua below Uruapan, Michoacán. Note epiphytes. June, 1958.

FIG. 1. Oak-bunchgrass association, 11.5 kilometers north of Cherán, Michoacán. June, 1955.

FIG. 2. Fir forest at Mil Cumbres, Michoacán. Bunchgrass and *Baccharus* are in the foreground. August, 1960.

see Brand (1960:50)]. Leavenworth (1946) described "cloud forest" on Cerro de Tancítaro, characterized by many epiphytes, mosses, and lichens in a predominantly pine-oak association. This forest is entirely different from the cloud forest in eastern México as described by Sharp (1946) and Martin (1958a). These workers define cloud forest, not only on structure, but on floral composition, which includes *Liquidambar, Magnolia, Tilia, Cornus, Fagus,* and in the understory tree ferns. Obviously, the problem here is one of definition. Floristically, two entirely different elements are represented; structurally, the cloud forests of eastern México and that on Cerro de Tancítaro show some similarity. Some of the features important for an animal habitat are present in both. Areas of cloud forest, whether in eastern México or on high mountains in western México, are characterized by high humidity resulting from rains throughout the year and from the presence of a bank of fog or clouds. Other common characteristics are relatively cool temperatures, bromeliads and other epiphytic plants, and a deep layer of mulch on the ground. The bromeliads and mulch form important habitats for plethodontid salamanders, certain hylid frogs, arboreal members of the genus *Eleutherodactylus,* lizards of the genus *Abronia,* and many small terrestrial snakes, such as *Rhadinaea, Pliocercus,* and *Micrurus.*

In this review of the vegetation of Michoacán the humid forests characterized by many epiphytes are discussed under the category of pine-oak forest and are not considered to be true cloud-forests. The cloud forests of eastern México differ significantly (floristically and structurally) as do their herpetological inhabitants.

Arid Tropical Scrub Forest

With the exception of the lower seaward slopes of the Sierra de Coalcomán, the lowlands—both coastal and inland in the Balsas-Tepalcatepec Basin—are covered with a low, xerophilous, deciduous thorn scrub forest, which in places forms dense nearly impenetrable thickets and in others presents a savanna appearance. In the coastal area scrub forest sometimes is restricted to the narrow coastal plain; in other areas it extends onto the foothills, sometimes to elevations of 300 to 400 meters. In the Balsas-Tepalcatepec Basin the scrub forest covers most of the broad valley floor and ascends the slopes to elevations of 600 to 1000 meters, depending on local conditions. At higher elevations the arid tropical scrub forest is replaced by oak, pine-oak, or tropical semi-deciduous forest.

The general appearance of the open scrub forest of much of the Tepalcatepec Valley and the dense scrub forest of the same valley and on the coastal plain will be described separately. The open scrub forest of the Balsas-Tepalcatepec Basin is characterized by low, xerophilous trees, most of which do not exceed six meters in height. In many places the trees are spaced 10 to 15 meters apart, and even when they are in full leaf only a small percentage of the ground is shaded. In this open forest many giant cacti, principally *Cephalocereus,* are ten meters high (Pl. 3, Fig. 2). Common trees in this open scrub forest are *Acacia cymbispina, Apoplanesia paniculata, Cercidium plurifoliolatum, Crescentia alata, Guaiacum coulteri, Mimosa distachya, Prosopis juliflora,* and *Zizyphus sonorensis.* In the dry season the trees are leafless, and the ground cover is dead grass. Shortly after the onset of the rains in early

summer the forest becomes green with the rapid growth of leaves and grasses (Pl. 4, Fig. 1).

The dense scrub forest of the valley and the coast differs from the open scrub forest chiefly in the close placement of the trees and in places higher forest. In many places the trees are so closely placed that it is impossible to pass through the forest; often the branches are so intermingled as to form an impenetrable tangle. In some places the crowns of the trees are as high as ten meters above the ground. The density of the scrub forest apparently is correlated with the amount of available water in the soil. In the Tepalcatepec Valley the open scrub forest is found on the valley floor away from the Río Tepalcatepec and its tributaries. Near streams and in many places on the slopes surrounding the valley the forest is dense. Possibly the dense scrub forest on the coast is the result of slightly higher rainfall, a higher water table, or an abundance of more species of trees capable of greater growth under xeric conditions.

With the exception of *Cercidium*, the trees of the open scrub forest are associated with the following species and form the dense scrub forest in the Balsas-Tepalcatepec Basin: *Bursera jorullensis, Caesalpina platyloba, Celtis iguanaea, Colubrina heteroneura, Cordia eleganoides, Cyrtocarpa procera, Diphysa floribunda, jaquinia pungens, Malpighia mexicana,* and *Nimosa spirocarpa.* The coastal scrub forest is physiognomically similar to the dense scrub forest of the interior basin; however, there are certain floristic differences; for example, *Apoplanesia paniculata* and *Cercidium plurifoliolatum,* both abundant and easily recognizable in the interior basin, are noticeably absent in the coastal forest. Abundant and widespread species in the coastal scrub forest are *Acacia cymbispina, Bursera sphaerocarpa, Caesalpina platyloba, Cassia atomaria, Cassia emarginata, Celtis iguanaea, Cordia dentata, Erythroxylon mexicanum, Erythroxylon pallidum, Guazuma ulmifolia, Jaquinia aurantiaca, Mimosa pigra, Mimosa rosei, Pithecoctenium echinatum, Pithecollombium lanceolatum,* and *Prosopis chilensis.* Scattered throughout the scrub forests, especially the open scrub forest in the Tepalcatepec Valley, are cacti—*Acanthocereus pentagonus, Pachycereus pecten-aboriginum,* and various species of *Opuntia.* Wherever the presence of sufficient water permits their development gigantic *Ficus, Enterolobium cyclocarpum,* and other large trees stand high above the surrounding scrub forest.

As an animal environment the scrub forest provides only limited shelter in the dry season, at which time some trees near streams may retain their leaves and thereby offer a limited amount of shade. There is an almost complete lack of ground cover, except in autumn when grasses and small herbs have reached their maximum growth. Known retreats for many species of snakes and lizards include rodent burrows and hollow branches of trees, notably *Apoplanesia paniculata.*

Tropical Semi-deciduous Forest

This type of forest, which is composed of species either having their distributions southward into the principal areas of tropical evergreen forest or having their relationships with species occurring in the tropical evergreen forest, is well developed on the lower windward slopes of the Sierra de Coalcomán. In sheltered areas along streams between promontories this type of

forest grows on the coastal plain, and in some barrancas and valleys occurs upward to an elevation of about 1000 meters. Usually it occurs between 150 and 600 meters. Probably the forest is discontinuous along the front of the Sierra de Coalcomán. Apparently this type of forest develops only in areas having deep soils and an abundant supply of water, either through heavy rainfall or ground water.

Physiognomically the forest consists of many large trees with crowns 25 to 30 meters above the ground; in some places in the rainy season the coverage is so complete that little sunlight reaches the ground, resulting in a poorly developed herbaceous layer. In the dry season some species drop their leaves at various times, but apparently at no time does the forest have a leafless appearance. Towards the end of the dry season, in early May, the majority of the trees in this type of forest near El Ticuiz and near La Placita have leaves. Although often there is not a well-developed herbaceous layer, an important micro-habitat in the form of leaf mulch is present. Climbers and lianas, especially in some of the coastal barrancas, such as Barranca de Bejuco and Barranca de Herradero, are more nearly characteristic of this type of forest than of any other in Michoacán. Also, some epiphytic plants are present (Pl. 4, Fig. 2).

Floristically the tropical semi-deciduous forest is characterized by many species of trees, none of which is dominant. Among the abundant large trees are the buttressed figs, *Ficus mexicana* and *Ficus padifolia;* other large members of the Moraceae include *Brosimum alicastrum* (locally known as uje), and *Castilla elastica* (ule). Also common and widespread are *Bombax ellipticum* (pochote), *Ceiba aesculifolia, Ceiba parvifolia, Licania arborea* (cacahuananche), *Sideroxylon capiri* (capiri), and two species of trees having smooth trunks and thin reddish peeling bark known as papelillo or palo colorado—*Trichilia hirta* and *Bursera simaruba.* Conspicuous legumes in this forest are *Haematoxylon brasiletto* and *Enterolobium cyclocarpum,* known as parota (Pl. 5, Fig. 1). Other abundant trees include *Anona purpurea, Astianthus viminalis, Coccoloba uvifera, Hura crepiten, Leucopremna mexicana, Lonchocarpus lanceolatus, Plumeria rubra, Tabebuia* sp., and *Swietenia* sp. Among the climbers the most widespread and abundant seem to be *Philodendron* sp., climbing cacti of the genera *Aporocactus* and *Selenicereus,* and several species of *Monstera.*

Relicts of this type of forest are in barrancas and valleys on the lower slopes of the Cordillera Volcánica north of the Tepalcatepec Valley. Furthermore, members of this forest community form the gallery forests along the larger streams in the Tepalcatepec Valley. In these areas typical representatives are *Ficus mexicana, Ficus padifolia, Sideroxylon capiri, Brosimum alicastrum, Bursera simaruba,* and *Enterolobium cyclocarpum.* The gallery forests are developed only along permanent streams in the Tepalcatepec Valley. Here too are found many species typical of the arid scrub forest of the valley proper. These trees often reach gigantic proportions in the gallery forest; especially noticeable are species of *Pithecolobium, Lysiloma,* and *Acacia.*

As an animal habitat the tropical semi-deciduous forest is important in that it provides a mesic environment. The large trees offer not only an extensive arboreal habitat, but an abundance of shade. The presence of a mulch layer is of obvious significance as an animal habitat.

Mesquite-Grassland

The high tableland comprising the southern part of the Mexican Plateau or Mesa Central has a vegetation distinctly different from that found in the mountains bordering or rising from the plateau, or that found in the lowlands. In Michoacán mesquite-grassland exists at elevations from about 1500 meters near Lago de Chapala in the northwestern part of the state to 2000 meters at Zacapu and 2100 meters near Ciudad Hidalgo to the east.

According to Leopold (1950), who proposed the term "mesquite-grassland," much of the region in Jalisco, Michoacán, and Guanajuato probably originally supported a vegetation of bunch-grasses. Now, however, many areas are only sparsely covered with grasses; instead the dominant plants are legumes and cacti or agave. This change is probably due to human intervention in natural phenomena, such as the reduction of grass fires, and to overgrazing. As has been shown by Glendening (1952) and Humphrey and Mehrhoff (1958), reduction of range fires and increase in grazing has been responsible for the invasion of semi-desert grassland in southern Arizona by desert plants, such as mesquite, creosote bush, and cholla. Although a rocky hillside covered with scattered *Opuntia, Prosopis, Acacia,* and *Fouquieria* does not give the appearance of a mesquite-grassland, the term is used here for the lack of a better name and for the reasons stated above.

Physiognomically true mesquite-grassland where it occurs in Michoacán consists of almost pure grassland like that near Morelia and that south of Jiquilpan (Pl. 5, Fig. 2). In other areas there are scattered legumes. However, most of the plateau vegetation consists of the successional stage consisting of legumes, cacti, and agave (Pl. 6, Fig. 1). Normally the tallest trees are less than ten meters high and scattered, but in some places form clumps. In the dry season most of the legumes and other trees are leafless, and the leaf blades of the grasses that in some areas formed a nearly continuous ground cover in the rainy season are dead.

Floristically the true mesquite-grassland as it occurs in Michoacán consists of *Prosopis, Mimosa, Eysenhardtia,* and *Acacia,* together with the grasses *Bouteloua* and *Muhlenbergia.* Other associations include *Argemone-Asclepias-Baccharis, Agave-Senecio-Baccharis,* and *Asclepias-Solanum-Acacia-Mimosa.* In the areas where this vegetation has been replaced by a more xeric type there are several species of *Agave* and *Opuntia,* and in some places *Yucca decipiens.* Some of the *Opuntia* develop into trees attaining heights of five or six meters. The principal scrubby trees are *Prosopis;* other small trees and shrubs include *Acacia* sp., *Brongniartia inconstans, Bursera microphylla, Bursera odorata, Euphorbia calyculata, Erythrine* sp., *Fouquieria formosa, Hyptis albida, Ipomoea murucoides, Zexmenia michoacana,* and some scrubby *Quercus.* There are stands of low *Juniperus* in some places.

Along streams on the plateau there are trees as tall as 15 to 20 meters; *Taxodium* and *Salix* occur in these riparian situations.

The mesquite-grassland provides an animal habitat similar to that of the arid tropical scrub forest; however, the mesquite-grassland is characterized by lower temperatures and usually by slightly more precipitation, as well as occasional frosts. On the Mexican Plateau, as in the Tepalcatepec Valley, the vegetation offers little shade and provides little in the way of shelter for animals.

Pine-oak Forest

Combined in this category are pine forests, oak forests, and pine-oak forests; because the animal habitats are generally alike, for the purposes of this study these types of forests have been grouped together. Pine and oak forest forms the dominant vegetation in the highlands of Michoacán. Altitudinally this type of forest is found from about 1000 meters to 4000 meters. At lower elevations it is replaced by arid tropical scrub forest, tropical semideciduous forest, or mesquite-grassland; usually above about 2700 meters it is replaced by fir, although in some places pine or pine-oak forest becomes dominant again at still higher elevations. There are large expanses of this kind of forest in the Cordillera Volcánica and in the Sierra de Coalcomán. Pine-oak forest grows on a variety of soils, many of which are volcanic or notably stony. In many places nearly pure stands of oak, usually scrubby, frequently with an understory of bunchgrass (*Muhlenbergia*), intervene between pine forest and arid tropical scrub forest or mesquite-grassland. At higher elevations oaks and pines are mixed, or oaks are absent. Pure stands of oak above 1200 meters are rare unless the forest is a transition between pine forest and mesquite grassland or unless the oaks are a successional stage on recently formed volcanic soils. Above 2400 meters oak and pine are frequently mixed with fir. The general nature of the pine-oak forest usually is subhumid, but there are some striking exceptions. In the dry season the oaks drop their leaves; the ground in pine-oak forest often has a layer of oak leaves, pine needles, or both.

The physiognomy of the forest varies from place to place. Between Carapan and Uruapan in the Sierra de los Tarascos nearly pure stands of pine averaging about 25 meters high include some trees 30 meters tall. Generally, because of heavy grazing by goats and other livestock, there is no lower story, except for grasses and scattered pine seedlings. Similar pine forests occur in the Sierra de Coalcomán (Pl. 6, Fig. 2). At an elevation of 2100 meters at Dos Aguas in the Sierra de Coalcomán, a seemingly virgin pine-oak forest has pines more than 35 meters high with girths of more than a meter. Large oaks, some of which attain heights of 30 meters, are scattered among the pines; in some places the oaks are dominant. The understory consists of various herbs and bushes, principally *Baccharis,* as well as oak and pine seedlings and saplings. The forest at Dos Aguas is on a windward ridge frequently bathed in clouds. Thick mats of mosses and lichens on the trees, and many epiphytes, including large bromeliads and orchids, grow in abundance (Pl. 7, Fig. 1). There is a deep layer of mulch on the ground. This is the "cloud forest" of Leavenworth (1946). Similar humid pine-oak forest is on Cerro El Cantor near Las Tecatas and on Cerro Bolo in the Sierra de Coalcomán, and on the windward slopes of Cerro de Tancítaro. Between 1200 and 1400 meters on the slopes of the Cordillera Volcánica below Uruapan oaks are the dominant trees, attaining heights of about 20 meters. There are many smaller oaks, occasional trees belonging to the scrub forest lower on the slopes, and a ground cover of sparse grasses. Small bromeliads are locally abundant (Pl. 7, Fig. 2). Similar extensive oak forests grow at elevations between 1000 and 1500 meters in the eastern part of the Sierra de Coalcomán, especially in the hills to the south and southwest of Arteaga, and between 1600 and 2000 meters between Tzitzio and Temazcal on the slopes of the Cordillera Volcánica. Near Cherán and between Carapan and Quiroga

in the Sierra de los Tarascos some areas are dominated by scrubby oaks reaching heights of about 10 meters and bunchgrass (*Muhlenbergia*) (Pl. 8, Fig. 1). Possibly this association is a successional stage on the volcanic soils; its present condition affords a somewhat different animal habitat from the surrounding pine or pine-oak forest.

Floristically the forest consists principally of various species of oaks and pines. Of the oaks, *Quercus macrophylla* is the dominant tree in the oak forest below Uruapan; *Q. calophylla, Q. crassifolia,* and *Q. decipiens* occur in the pine-oak forests in the Sierra de los Terascos. According to Brand (personal communication), 12 species of oaks occur in the area around Quiroga; the most abundant species there are *Q. obtusata, Q. reticulata,* and *Q. vellifera. Pinus montezumae* and *P. oöcarpa* seem to be among the most abundant and widespread pines in the Cordillera Volcánica and the Sierra de Coalcomán. *Pinus hartwegii* also occurs in the Sierra de Coalcomán. In the mountains around Lago de Pátzcuaro the species of pines in approximate order of decreasing abundance are *Pinus leiophylla, P. michoacana, P. montezumae, P. pseudostrobus, P. lawsoni,* and *P. pringlei* (Brand, personal communication). Alders (*Alnus arguta* and other species), madroño (*Arbutus xalapensis*), *Clethra, Crataegus,* and some *Tilia* frequently are mixed with the pines and oaks. If an understory is present, it often consists of a species of *Baccharis;* the ground layer frequently is composed of ferns (*Pteris*), lupines, thistles, *Astragalus,* and Umbelliferae. Grasses in the pine-oak forest usually are *Muhlenbergia* and *Bouteloua.* At least in the Cordillera Volcánica, the small broad-leafed herb, *Senecio tolucanus,* is a common species in the ground layer.

Highly diversified as it is, the pine-oak forest provides a variety of animal habitats. The trees are inhabited by a number of species of lizards. The leaf and needle litter, which in depressions often accumulates to a depth of several centimeters, affords shelter for many small terrestrial animals. Bromeliads provide a habitat found elsewhere in the state only to a limited extent in the tropical semi-deciduous forest.

Fir Forest

In the higher reaches of the major mountain ranges isolated areas of fir forest are found on Cerro de Barolosa in the Sierra de Coalcomán and on Cerro de Tancítaro, Cerro Patambán, Cerro Zirate, Cerro San Andrés, the area of the Mill Cumbres, and in the area of Puerto Hondo in the Sierra Temazcaltepec near the border of the state of México. Normally stands of fir forest are found only above 2400 meters and most frequently above 2700 meters. In ravines on north facing slopes scattered firs are found as low as 2000 meters, but these are not in the fir forest proper.

Pure stands of fir are of local occurrence; generally the fir is mixed with pine and sometimes oak. In some of the virgin fir and pine-fir forests the trees reach heights of 40 meters. Often the trees are closely spaced and provide a high percentage of coverage (Pl. 8, Fig. 2). In other areas, especially where the fir is mixed with pine and oak, the trees are more widely spaced.

Floristically the forest consists of fir (*Abies religiosa*); pines, *P. hartwegii, P. oöcarpa,* and *P. montezumae,* usually are present with the last species the most abundant. In some areas various species of *Quercus* and *Alnus* occur

with the fir. If an understory is present, it usually consists of one or more species of *Baccharis,* thistles, lupines, bunchgrasses and various ferns. Mosses are abundant.

Because of the low temperatures and high humidity, fir forest presents an environment different from all others in Michoacán. Although the humidity is high, the cool temperatures do not permit rapid decay; consequently, there usually is a deep layer of needles and humus on the forest floor. These form an important microhabitat for many small animals, especially the plethodontid salamanders.

Minor Vegetation Types and Animal Habitats

Either because of their limited extent or artificial nature, certain distinct vegetation types and animal habitats have not been included in the above classification of the major vegetation types nor shown on the accompanying map. These minor habitats include the various aquatic or semi-aquatic habitats, ocean beaches, and unnatural but important animal habitats such as coconut plantations and irrigated fields.

As stated previously, most of the coast of Michoacán consists of small beaches separated by promontories; in the western part of the state from the Río Coahuayana to Punta San Juan de Lima, and in the eastern part from Las Peñas to the mouth of the Río Balsas there are extensive beaches and a narrow coastal plain. In these areas mangrove swamps surround brackish lagoons. Also, on these coastal plains there are coconut plantations.

Beaches.—According to Brand (1958), two abundant species of vines, *Ipomoea pes-caprae* and *Canavalia maritima* form a transitional vegetation between the barren sand beaches and the arid tropical scrub forest; other common plants in this association are *Capparis, Lantana, Phaseolus, Stegnosperma,* and *Cenchrus echinata.*

Mangrove Swamps.—Mangroves occur sporadically along the coast, and four species make up extensive swamps surrounding lagoons in at least two places on the coast of Michoacán—Laguna Mexcala near El Ticuiz and Estero Pichi near Playa Azul. At both places mangroves noted were: *Conocarpus erecta, Rhizophora mangle, Laguncularia racemosa,* and *Avicennia nitida.* Brand (1958) noted that *Hibiscus tiliaceus* was a common tree among the mangroves at Laguna Mexcala.

Palmares.—Near Ojos de Agua de San Telmo is a large grove of oil palms (*Orbignya cohune*); other such palm groves occur near San Blas in Nayarit, at Bahía Banderas in Jalisco, around Laguna Cuyutlán in Colima, and on the Zacatula Delta in Guerrero.

Marshes.—Freshwater marshes are found along the eastern shore of Lago de Pátzcuaro, at Lago de Cuitzeo, Ixtlán de los Hervores, Laguna Verde, in the Río Duero basin near Zamora, and around Lago de Chapala. Today the last mentioned marshes are small, but once were large. Goldman (1951) stated that in 1903 the marshes near the mouth of the Río Lerma were probably the largest and most important freshwater marshes in all of México. In the period 1909 to 1912 a dike was built across the eastern edge of Lago de Chapala; this resulted in the draining and evaporation of water from thousands of square kilometers of marshland, now under cultivation.

Coconut Plantations.—In some areas along the coast, chiefly near Coahuayana and Playa Azul, the original arid tropical scrub forests, or possibly oil palm forest, has been cleared, and coco palms (*Cocos nucifera*) have been planted there, thus providing an open and sunny environment as contrasted with that of the denser surrounding scrub forest.

Irrigated Fields.—Many irrigation ditches support water hyacinths (*Eichhornia*) and cat-tails (*Typha*). Irrigated fields in otherwise arid areas provide optimum conditions for some amphibians, such as *Bufo marinus, Hyla smithi* and *Leptodactylus melanonotus* even in the dry season.

Lakes and Streams.—The large lakes on the Mexican Plateau provide some of the most extensive freshwater habitat in all of México. In Michoacán most streams drop in level in the dry season; some become intermittent, and others dry up entirely. Along stream courses, especially in shaded places, elephant-ear plants (*Xanthosoma*) are a favorite refuge for small frogs, such as *Hyla smaragdina* and *Hyla smithi.*

COMPOSITION OF THE HERPETOFAUNA

The herpetofauna of Michoacán is composed of 166 species definitely recorded, plus nine others that probably occur in the state. Ten of the species have two or more subspecies in the state; therefore, the total herpetofauna probably consists of 185 species and subspecies. The fauna is made up of six species (3.4% of the total number of species) of salamanders, 40 (22.9%) anurans, six (3.4%) turtles, one (0.6%) crocodilian, 48 (27.4%) lizards, and 74 (42.3%) snakes (Table 1). For its size (60,093 square kilometers), the state has many species. The diversity of the fauna is the result of variation in topography, presence of many habitats, and the geographical position of the state with regard to past faunal movements.

Table 1.—Composition of the Herpetofauna of Michoacán.

	Families	Genera	Species
Salamanders	2	2	6
Anurans	7	15	40
Turtles	3	4	6
Crocodilians	1	1	1
Lizards	8	18	48
Snakes	7	42	74

One snake (*Pelamis platurus*) and one turtle (*Chelonia mydas*) are marine and are not considered in the following discussion of geography and ecology.

ECOLOGY OF THE HERPETOFAUNA

In a preceding section (page 641) the major animal habitats in Michoacán were defined and delimited geographically. Here the herpetofauna within these habitats is analyzed in an essentially descriptive manner. Adequate data on the ecology of the amphibians and reptiles in Michoacán are available for only a few of the more abundant and conspicuous species.

In Michoacán the arid tropical scrub forest in the Tepalcatepec Valley was studied more intensively than any other habitat; then perhaps, in decreasing

order of study, were the pine-oak forests, mesquite-grassland on the Mexican Plateau, and the fir forests, and the tropical semi-deciduous forest. Amount of time spent in each of these habitats was generally proportional to the apparent diversity of the fauna, except for the tropical semi-deciduous forest, which because of its inaccessibility, was visited less frequently than the other habitats. Although nearly as much time was spent in the pine-oak forest as in the arid tropical scrub forest, probably less is known about the ecology of the fauna in the former than in the latter. The seasonal activity of the herpetofauna, tends to prevent an observer from gaining a complete picture of distribution, especially of the amphibians. An effort was made to visit the various habitats in different areas in both the wet and dry seasons. Although I spent many weeks in the Tepalcatepec Valley in three rainy seasons, I never found *Diaglena spatulata* or *Pternohyla fodiens* there; two years after my last visit James R. Dixon obtained both species there in one night. Probably man's influence in destroying habitats and creating new ones is of some importance in the ecological distribution of the herpetofauna, but, as will be discussed later, man seems not to have significantly altered the basic patterns of ecological distribution in Michoacán.

Distribution Within Habitats

The distribution of the species and subspecies is summarized in Table 2. In order to show the relative abundance of a species in a given habitat, each species in each habitat is designated as being abundant (A), moderately abundant (M), apparently rare (R), of questionable occurrence (?), or absent (—). Such a classification is highly subjective, but for species that occupy two or more habitats it shows to which habitat the species apparently are best adapted. Of course, availability of breeding sites and competition are significant in determining the relative abundance of a given species in certain habitats (see p. 664).

Arid Tropical Scrub Forest

Arid tropical scrub forest is the most extensive tropical habitat in Michoacán and occurs in two separate geographical areas—the Pacific coastal plain and the inland Balsas-Tepalcatepec Basis. Seventy-seven species and subspecies of amphibians and reptiles live in the arid tropical scrub forest; of these, 22 are considered abundant.

In the arid tropical scrub forest in the Tepalcatepec Valley the following species are characteristic and abundant:

Bufo marinus
Bufo perplexus
Leptodactylus labialis
Leptodactylus melanonotus
Hyla baudini
Hyla smithi
Ctenosaura pectinata
Sceloporus horridus
Sceloporus pyrocephalus
Urosaurus gadowi
Cnemidophorus calidipes
Cnemidophorus costatus
Cnemidophorus deppei
Drymobius margaritiferus
Leptodeira maculata
Salvadora mexicana
Thamnophis dorsalis

TABLE 2.—ECOLOGICAL AND ALTITUDINAL DISTRIBUTION OF AMPHIBIANS AND REPTILES IN MICHOACÁN.

(A, abundant; M, moderately abundant; R, apparently rare; ?, presence not established.)

SPECIES	Arid tropical scrub forest	Tropical semi-deciduous forest	Mesquite-grassland	Pine-oak forest	Fir forest	Altitudinal range in meters
Ambystoma amblycephalum	—	—	—	M	M	2300–2800
Ambystoma dumerili dumerili	—	—	—	R	—	2165
Ambystoma ordinarium	—	—	—	M	A	2400–3000
Ambystoma tigrinum velasci	—	—	—	R	—	2000–2200
Pseudoeurycea belli	—	—	—	A	M	1500–2900
Pseudoeurycea robertsi	—	—	—	—	A	2900–3000
Rhinophrynus dorsalis	R	—	—	—	—	0–10
Scaphiopus hammondi multiplicatus	—	—	A	M	—	1500–2500
Bufo coccifer	M	—	—	—	—	335–640
Bufo compactilis compactilis	—	—	M	—	—	1525–2050
Bufo marinus	A	M	—	—	—	0–1000
Bufo marmoreus	M	A	—	—	—	0–1000
Bufo occidentalis	—	—	—	A	R	900–2400
Bufo perplexus	A	—	—	—	—	180–1630
Leptodactylus labialis	A	—	—	—	—	180–1050
Leptodactylus melanonotus	A	M	—	—	—	0–1050
Leptodactylus occidentalis	—	—	R	—	—	1700
Microbatrachylus hobartsmithi	—	—	—	M	R	1450–2750
Microbatrachylus pygmaeus	—	A	—	—	—	850
Eleutherodactylus augusti cactorum	—	—	—	R	—	945–2350
Eleutherodactylus occidentalis	R	M	—	R	—	20–1500
Eleutherodactylus rugulosus vocalis	—	M	—	—	—	130–1630
Tomodactylus angustidigitorum	—	—	—	A	—	1500–2500
Tomodactylus fuscus	—	—	—	R	—	2100–2200
Tomodactylus nitidus nitidus	—	—	M	R	—	1200–1800
Tomodactylus nitidus orarius	—	M	—	—	—	20–300
Tomodactylus nitidus petersi	M	M	R	M	—	335-1630
Tomodactylus rufescens	—	—	—	M	—	1600–2100
Diaglena reticulata	R	—	—	—	—	120–330
Pternohyla fodiens	R	—	—	—	—	380
Phyllomedusa dacnicolor	A	M	—	—	—	0–1000
Phrynohyas inflata	—	R	—	—	—	90
Hyla arenicolor	R	M	—	M	—	500–2100
Hyla baudini	A	A	—	—	—	0–1200
Hyla bistincta	—	—	—	A	R	1600–2400
Hyla eximia	—	—	A	A	—	1500–2300
Hyla lafrentzi	—	—	—	R	M	2400–2800
Hyla microcephala sartori	—	?	—	—	—	?
Hyla smaragdina	—	M	R	M	—	150–1500
Hyla smithi	A	A	—	—	—	0–1000
Gastrophryne usta usta	?	—	—	—	—	?
Hypopachus caprimimus	M	—	R	—	—	200–1800
Hypopachus oxyrrhinus ovis	—	—	A	—	—	1500–2200
Rana dunni	—	—	M	M	—	2000–2165
Raya megapoda	—	—	M	—	—	1525
Rana montezumae	—	—	M	—	—	1500–2000
Rana pipiens	A	M	A	A	M	0–2800

TABLE 2.—ECOLOGICAL AND ALTITUDINAL DISTRIBUTION OF AMPHIBIANS AND REPTILES IN MICHOACÁN.—*Continued*

SPECIES	Arid tropical scrub forest	Tropical semi-deciduous forest	Mesquite-grassland	Pine-oak forest	Fir forest	Altitudinal range in meters
Rana pustulosa	—	M	—	M	—	850–2150
Kinosternon hirtipes hirtipes	—	—	M	—	—	1525–2160
Kinosternon integrum	A	M	A	M	—	0–2200
Geoemyda pulcherrima pulcherrima	?	—	—	—	—	?
Geoemyda rubida perixantha	R	—	—	—	—	0–635
Pseudemys scripta ornata	?	—	—	—	—	?
Crocodylus acutus acutus	M	—	—	—	—	0–10
Bipes canaliculatus	?	—	—	—	—	?
Coleonyx elegans nemoralis	?	?	—	—	—	?
Phyllodactylus duellmani	M	—	—	—	—	180–500
Phyllodactylus homolepidurus	—	M	—	—	—	0–500
Phyllodactylus lanei	—	A	—	M	—	0–1100
Phyllodactylus paucituberculatus	R	—	—	—	—	270
Anolis dunni	—	—	—	R	—	700–850
Anolis nebulosus	A	A	R	M	—	0–2100
Anolis schmidti	—	R	—	—	—	0–10
Basiliscus vittatus	M	A	—	—	—	0–350
Iguana iguana rhinolopha	M	M	—	—	—	0–800
Ctenosaura pectinata	A	M	—	—	—	0–1000
Enyaliosaurus clarki	A	—	—	—	—	200–510
Phrynosoma asio	R	—	—	—	—	300–700
Sceloporus aeneus aeneus	—	—	—	A	A	1850–3100
Sceloporus asper	—	R	—	M	—	335–1630
Sceloporus bulleri	—	—	—	A	—	2000–2350
Sceloporus dugesi intermedius	—	—	A	M	—	1500–2200
Sceloporus gadowae	M	—	—	—	—	250–1050
Sceloporus grammicus microlepidotus	—	—	—	A	M	1550–3100
Sceloporus heterolepis	—	—	—	M	R	1800–2700
Sceloporus horridus oligoporus	A	—	—	—	—	0–1600
Sceloporus melanorhinus calligaster	—	A	—	—	—	30–1500
Sceloporus pyrocephalus	A	—	—	—	—	0–1000
Sceloporus scalaris scalaris	—	—	M	M	—	1550–2300
Sceloporus siniferus siniferus	M	—	—	—	—	0–150
Sceloporus spinosus spinosus	—	—	M	—	—	1500–2300
Sceloporus torquatus torquatus	—	—	M	A	M	1450–3000
Sceloporus utiformis	—	M	—	M	—	0–1550
Urosaurus bicarinatus tuberculatus	—	M	—	M	—	0–1700
Urosaurus gadowi	A	—	—	—	—	180–1200
Mabuya brachypoda	M	M	—	—	—	0–1050
Scincella assata taylori	—	R	—	—	—	120–850
Eumeces altamirani	R	—	—	—	—	350–1050
Eumeces colimensis	—	R	—	—	—	130–950
Eumeces copei	—	—	—	R	R	1800–2700
Eumeces dugesi	—	—	—	A	M	1550–1850
Eumeces indubitus	—	—	—	R	—	2750
Eumeces parvulus	—	M	—	—	—	30–500
Ameiva undulata sinistra	—	A	—	—	—	10–950
Cnemidophorus calidipes	A	—	—	—	—	200–650
Cnemidophorus communis communis	A	—	—	—	—	10–950
Cnemidophorus costatus occidentalis	—	—	R	—	—	1570

Table 2.—Ecological and Altitudinal Distribution of Amphibians and Reptiles in Michoacán.—*Continued*

Species	Arid tropical scrub forest	Tropical semi-deciduous forest	Mesquite-grassland	Pine-oak forest	Fir forest	Altitudinal range in meters
Cnemidophorus costatus zweifeli	A	—	—	—	—	200–1100
Cnemidophorus deppei deppei	R	—	—	—	—	130–500
Cnemidophorus deppei infernalis	A	—	—	—	—	200–1050
Cnemidophorus lineatissimus exoristus	—	M	—	—	—	170–900
Cnemidophorus lineatissimus lineatissimus	—	R	—	—	—	0–10
Cnemidophorus lineatissimus lividus	—	A	—	—	—	0–500
Cnemidophorus scalaris	—	—	A	—	—	1600–1900
Heloderma horridum horridum	—	R	—	—	—	0–1000
Gerrhonotus imbricatus imbricatus	—	—	—	M	M	1500–3500
Typhlops braminus	R	R	—	—	—	335–850
Leptotyphlops bressoni	R	—	—	—	—	1050
Leptotyphlops gadowi	R	—	—	—	—	800
Leptotyphlops phenops bakewelli	—	R	—	—	—	0–850
Loxocemus bicolor	R	—	—	—	—	0–640
Boa constrictor imperator	M	M	—	—	—	0–1000
Clelia clelia	—	?	—	—	—	?
Coniophanes fissidens dispersus	—	R	—	—	—	850
Coniophanes lateritius lateritius	—	R	—	—	—	900
Conophis vittatus vittatus	M	—	—	—	—	800–1100
Conopsis biserialis	—	—	—	A	A	1550–2800
Conopsis nasus	—	—	—	M	R	1900–2450
Diadophis dugesi	—	—	—	R	—	1900–2200
Dryadophis melanolomus stuarti	—	M	—	—	—	0–50
Drymarchon corais rubidus	M	M	R	R	—	0–1350
Drymobius margaritiferus fistulosus	A	M	—	—	—	0–1150
Elaphe triaspis intermedius	M	—	R	—	—	350–1350
Enulius unicolor	—	M	—	—	—	900–1800
Geagras redimitus	—	R	—	—	—	10
Geatractus tecpanensis	?	—	—	—	—	?
Geophis dugesi	—	—	—	R	—	1750–2050
Geophis incomptus	—	—	—	M	—	2100
Geophis maculiferus	—	—	—	R	—	1630
Geophis nigrocinctus	—	—	—	R	—	2100
Geophis petersi	—	—	—	M	—	950–2350
Geophis tarascae	—	—	—	R	—	1630
Hypsiglena torquata ochrorhyncha	—	—	R	—	—	2300
Hypsiglena torquata torquata	R	—	—	—	—	200–350
Imantodes gemmistratus gracillimus	—	R	—	—	—	10
Imantodes gemmistratus latistratus	R	—	—	—	—	1050
Lampropeltis doliata	M	R	R	R	—	0–1900
Lampropeltis ruthveni	—	—	R	—	—	1900–2200
Leptodeira latifasciata	M	—	—	—	—	335–1050
Leptodeira maculata	A	M	—	—	—	0–1000
Leptodeira septentrionalis polysticta	—	?	—	—	—	?
Leptodeira splendida bressoni	R	M	—	R	—	950–1650
Leptophis diplotropis	—	M	—	R	—	850–1700
Manolepis putnami	—	M	—	—	—	20–120
Masticophis striolatus striolatus	M	—	R	—	—	0–1650
Masticophis taeniatus australis	—	—	R	—	—	1570–2000
Oxybelis aeneus auratus	—	A	—	M	—	0–1700

TABLE 2.—ECOLOGICAL AND ALTITUDINAL DISTRIBUTION OF AMPHIBIANS AND REPTILES IN MICHOACÁN.—*Concluded*

SPECIES	Arid tropical scrub forest	Tropical semi-deciduous forest	Mesquite-grassland	Pine-oak forest	Fir forest	Altitudinal range in meters
Pituophis deppei deppei	—	—	M	—	—	1900–2200
Pituophis lineaticollis lineaticollis	—	—	R	M	—	1500–2300
Pseudoficimia frontalis	M	—	—	—	—	330–1050
Pseudoficimia pulcherrima	R	—	—	—	—	330
Rhadinaea hesperia hesperia	R	M	R	—	—	850–1500
Rhadinaea laureata	—	—	—	A	—	1800–2300
Rhadinaea taeniata	—	—	—	R	—	1850
Salvadora bairdi	—	—	A	M	—	1550–2500
Salvadora mexicana	A	—	—	—	—	0–1000
Sibon nebulatus	—	R	—	—	—	150
Sonora michoacanensis michoacanensis	M	—	—	—	—	330–1000
Tantilla bocourti	—	—	—	M	R	2000–2200
Tantilla calamarina	R	—	—	—	—	20–330
Toluca lineata lineata	—	—	—	A	M	1550–2800
Trimorphodon biscutatus biscutatus	A	—	—	—	—	20–1050
Trimorphodon latifascia	M	—	—	—	—	300–1430
Trimorphodon tau	—	—	R	—	—	1600–2000
Tropidodipsas occidentalis	—	R	—	—	—	950
Natrix valida isabelleae	M	—	—	—	—	0–10
Storeria storerioides	—	—	—	M	R	1550–2800
Thamnophis dorsalis cyclides	—	—	M	A	R	1550–2800
Thamnophis dorsalis postremus	A	R	—	—	—	200–1550
Thamnophis eques eques	—	—	A	M	—	1550–2300
Thamnophis melanogaster canescens	—	—	M	—	—	1550–2200
Thamnophis scalaris scaliger	—	—	—	R	R	1800–3400
Micrurus distans michoacanensis	M	—	—	—	—	350
Micrurus laticollaris	R	—	—	—	—	500–1050
Agkistrodon bilineatus bilineatus	M	—	—	—	—	300–1500
Crotalus basiliscus basiliscus	M	—	—	—	—	20–1070
Crotalus durissus culminatus	M	—	—	—	—	1050
Crotalus intermedius intermedius	—	—	—	R	—	2200
Crotalus molossus nigrescens	—	—	—	M	—	1550–2300
Crotalus polystictus	—	—	R	—	—	1450–2400
Crotalus pusillus	—	—	—	A	—	1550–2300
Crotalus triseriatus aquilus	—	—	M	M	—	1600–2000
Crotalus triseriatus triseriatus	—	—	—	A	—	1600–3270

In the same habitat on the Pacific coastal plain the following species are characteristic:

Bufo marinus
Bufo marmoreus
Leptodactylus melanonotus
Hyla baudini
Hyla smithi
Anolis nebulosus
Basiliscus vittatus
Ctenosaura pectinata
Sceloporus horridus
Sceloporus pyrocephalus
Sceloporus siniferus
Leptodeira maculata

Characteristically the species inhabiting the arid tropical scrub forest are adapted for life in open, subhumid conditions. Diurnal species usually are fast and agile, such as *Drymobius margaritiferus, Masticophis striolatus, Salvadora mexicana, Basiliscus vittatus, Sceloporus siniferus,* and the various species

of *Cnemidophorus*. Saxicolous diurnal species inhabiting natural rock outcroppings or stone walls include, among others, *Ctenosaura pectinata, Sceloporus gadowae, Sceloporus horridus,* and *Sceloporus pyrocephalus.* Few diurnal species are arboreal, but *Enyaliosaurus clarki* lives in scrubby trees, and *Urosaurus gadowi* inhabits the trunks of small trees in the scrub forest.

Many species inhabiting the arid tropical scrub forest are nocturnal. In this category are all of the anurans, of which *Bufo marinus, Leptodactylus melanonotus, Hyla baudini,* and *Hyla smithi* are the most widespread. Common nocturnal snakes are *Leptodeira latifasciata, Leptodeira maculata, Pseudoficimia frontalis, Thamnophis dorsalis, Trimorphodon biscutatus, Trimorphodon latifascia, Micrurus distans, Micrurus laticollaris,* and *Crotalus basiliscus.* Of the lizards, only *Phyllodactylus duellmani* and *Phyllodactylus paucituberculatus* are noctural. A higher percentage of species in the arid tropical scrub forest is nocturnal than in the other habitats in Michoacán, probably because the nocturnal temperatures in that forest are optimal for many species. Some, for example *Drymarchon corais* and *Drymobius margaritiferus,* are diurnal in many parts of their geographic ranges but are at least partly noctural in the arid tropical scrub forest in the Balsas-Tepalcatepec Basin. In the pine-oak forest *Thamnophis dorsalis cyclides* is strictly diurnal, whereas the subspecies, *T. dorsalis postremus,* is nocturnal in the arid tropical scrub forest in the lowlands.

The lack of a well-developed humus layer on the ground in the arid tropical scrub forest apparently excludes some of the small semi-fossorial species, such as *Eumeces colimensis, Eumeces parvulus, Scincella assata,* and *Enulius unicolor.* Likewise, the absence of an extensive arboreal habitat precludes the presence of such species as *Sceloporus melanorhinus, Leptophis diplotropis,* and *Oxybelis aeneus,* or greatly restricts their distributions.

Tropical Semi-deciduous Forest

The tropical semi-deciduous forest occurs in small isolated patches on the windward slopes at low elevations. Sixty-two species occur in this habitat; of these, only 11 can be considered abundant there. The great amount of vegetational cover in this kind of forest provides ready concealment for most small animals, consequently many species that seem to be uncommon possibly are abundant.

Characteristic inhabitants of the tropical semi-deciduous forest include:

Microbatrachylus pygmaeus
Eleutherodactylus rugulosus
Phyllomedusa dacnicolor
Phyllodactylus lanei
Anolis nebulosus
Basiliscus vittatus
Sceloporus melanorhinus
Sceloporus utiformis
Eumeces parvulus
Ameiva undulata
Cnemidophorus lineatissimus
Dryadophis melanolomus
Leptophis diplotropis
Manolepis putnami
Oxybelis aeneus
Rhadinaea hesperia

Most species inhabiting the tropical semi-deciduous forest are tolerant of hot, humid conditions. Many species, such as *Microbatrachylus pygmaeus, Eumeces parvulus, Scincella assata, Enulius unicolor,* and *Rhadinaea hesperia,* inhabit the mulch on the forest floor. Others, including *Ameiva undulata, Cnemidophorus lineatissimus,* and *Dryadophis melanolomus,* actively move about on the forest floor, whereas *Phyllomedusa dacnicolor, Anolis nebulosus,*

Leptophis diplotropis, and *Oxybelis aeneus* are primarily arboreal. The well-developed arboreal microhabitat in the tropical semi-deciduous forest is inhabited by approximately 25 per cent of the species there; this is a higher percentage than in other habitats in the state. Apparently, because of the rather equable terrestrial climate in the tropical semi-deciduous forest, a relatively high percentage of species there are diurnal. The shade provided by the dense foliage results in a darkened forest floor having minimal evaporation; consequently, small amphibians, such as *Eleutherodactylus rugulosus* and *Microbatrachylus pygmaeus* often are abroad by day.

Mesquite-Grassland

The scrubby vegetation occurring on the Mexican Plateau provides a definitely subhumid habitat characterized by warm days and cool nights. Of the 39 species of amphibians and reptiles comprising the impoverished fauna there, only nine can be considered abundant. Among the characteristic species in this ecological assemblage are:

Scaphiopus hammondi
Bufo compactilis
Hyla eximia
Hypopachus oxyrrhinus
Sceloporus dugesi
Sceloporus spinosus
Cnemidophorus scalaris
Pituophis deppei
Salvadora bairdi
Thamnophis eques
Thamnophis melanogaster
Crotalus triseriatus

Most of the species inhabiting the mesquite-grassland are terrestrial; the uncommon *Hyla smaragdina,* which takes refuge in small bromeliads in low trees, is arboreal. The primarily terrestrial *Anolis nebulosus,* an invader from the lowlands, often sleeps in bushes at night. The anurans are active chiefly at night; some snakes, such as *Elaphe triaspis, Hypsiglena torquata,* and *Trimorphodon tau,* characteristically are nocturnal.

In the mesquite-grassland the margins of the several lakes on the Mexican Plateau form an important microhabitat. *Rana dunni, Rana megapoda, Rana montezumae, Thamnophis eques,* and *Thamnophis melanogaster* are typical inhabitants of those aquatic margins.

Pine-Oak Forest

The pine-oak forest is the most varied and extensive habitat in Michoacán and occurs in two areas—the Cordillera Volcánica and the Sierra de Coalcomán. Seventy species are known to inhabit the pine-oak forest; of these, only 17 are considered abundant there. In the pine-oak forest in the Cordillera Volcánica the following species are characteristic:

Pseudoeurycea belli
Bufo occidentalis
Microbatrachylus hobartsmithi
Tomodactylus angustidigitorum
Hyla bistincta
Hyla eximia
Sceloporus aeneus
Sceloporus grammicus
Sceloporus torquatus
Eumeces dugesi
Gerrhonotus imbricatus
Conopsis biserialis
Geophis petersi
Pituophis lineaticollis
Rhadinaea laureata
Toluca lineata
Storeria storerioides
Thamnophis dorsalis
Crotalus molossus
Crotalus pusillus

In the Sierra de Coalcomán the following species inhabit the pine-oak forest:

Bufo occidentalis
Tomodactylus rufescens
Hyla bistincta
Anolis nebulosus
Sceloporus bulleri
Sceloporus heterolepis
Gerrhonotus imbricatus
Geophis incomptus
Geophis nigrocinctus
Pituophis lineaticollis
Storeria storerioides
Thamnophis dorsalis
Crotalus pusillus

In the pine-oak forest the well-developed broad-leaf and pine needle mulch on the forest floor forms an important microhabitat for such semi-fossorial species as *Pseudoeurycea belli, Microbatrachylus hobartsmithi, Eumeces copei, Eumeces dugesi, Eumeces indubitus, Gerrhonotus imbricatus, Conopsis biserialis, Geophis dugesi, Geophis incomptus, Geophis nigrocinctus, Geophis petersi, Rhadinaea laureata, Tantilla bocourti, Toluca lineata,* and *Storeria storerioides.*

Lizards of the genus *Sceloporus* are the most conspicuous herpetological inhabitants of the pine-oak forest. In the Cordillera Volcánica *Sceloporus aeneus* is the common terrestrial species; *S. grammicus* is the ever-present arboreal species, whereas the larger *S. torquatus* lives on tree trunks and the ground alike. In the Sierra de Coalcomán *Sceloporus heterolepis* is the strictly arboreal species, and *S. bulleri* occurs as frequently on the ground as in the trees.

Of the snakes and lizards occurring in the pine-oak forest, only about one-third of the species tend to be nocturnal. Many of these, such as *Rhadinaea laureata* and *Toluca lineata,* are mulch-inhabitants that apparently move about mostly at night. The four species of *Crotalus* inhabiting the pine-oak forest are partly nocturnal. *Phyllodactylus lanei,* the only nocturnal lizard in this habitat, occurs only at low elevations in the pine-oak forest. As in the mesquite-grassland, the relatively low nocturnal temperatures preclude much activity by snakes at night.

Fir Forest

This cool, moist habitat characterized by a deep, moist layer of mulch on the ground is discontinuous in Michoacán. Patches of fir forest of varying areal dimensions occur on the highest mountains in the Cordillera Volcánica and in the Sierra de Coalcomán. Of the 23 species of amphibians and reptiles known to occur in the fir forests in Michoacán, only four can be considered abundant there. Characteristic inhabitants of the fir forests in the Cordillera Volcánica are:

Ambystoma ordinarium
Pseudoeurycea belli
Pseudoeurycea robertsi
Hyla lafrentzi
Sceloporus aeneus
Sceloporus grammicus
Sceloporus torquatus
Eumeces dugesi
Gerrhonotus imbricatus
Conopsis biserialis
Toluca lineata

In the fir forests of the Sierra de Coalcomán the list is much smaller; possibly this is due to less extensive collecting there. Known inhabitants of the fir forest in the Sierra de Coalcomán are *Bufo occidentalis, Sceloporus heterolepis, Gerrhonotus imbricatus,* and *Storeria storerioides.*

The only arboreal inhabitants of the fir forests are *Sceloporus grammicus, S. heterolepis,* and *S. torquatus,* all of which are more widespread and abundant in pine forests at lower elevations. The other inhabitants of the fir forests are

equally divided between mulch inhabitants, such as the various salamanders, *Eumeces dugesi, Conopsis biserialis,* and *Toluca lineata,* and terrestrial species, such as *Sceloporus aeneus* and the various species of *Thamnophis.* All of the lizards are strictly diurnal, as are all of the snakes with the possible exception of some of the mulch inhabitants.

Altitudinal Distribution

In an area having such varied topography as Michoacán, different altitudinal distributions among the species are expected. The known altitudinal ranges of the amphibians and reptiles in the state are given in Table 2. Examination of this table reveals that of the 183 species and subspecies listed therein, only 43 have altitudinal ranges of 1000 meters or more; of those, only five species (*Rana pipiens, Kinosternon integrum, Anolis nebulosus, Gerrhonotus imbricatus,* and *Thamnophis dorsalis*) have altitudinal ranges of 2000 meters or more.

An analysis of the limits of altitudinal distribution of the various species (Fig. 4) shows that the upper and lower limits of distribution of many species are reached at certain elevations, whereas fewer distributional limits occur at intermediate elevations. Of course, a large number (53) of species have the lower limits of their distributions at or near sea level. The lower limits of the altitudinal distributions of several other species approach sea level, but terminate between 100 and 200 meters above it on the slopes of the Sierra de Coalcomán. In this group are some frogs, such as *Eleutherodactylus rugulosus* and *Hyla smaragdina,* which live along streams having moderately steep gradients, and certain lizards and snakes, such as *Scincella assata, Eumeces colimensis,* and *Sibon nebulatus,* which do not inhabit the arid tropical scrub forest on the coastal plain. The group of species having their lower limits of altitudinal distribution at about 300 meters is primarily made up of those species that reach the lower limits of their distributions in the Tepalcatepec Valley and do not live on the coastal lowlands. Common species in this group are:

Bufo perplexus
Hypopachus caprimimus
Phyllodactylus duellmani
Enyaliosaurus clarki
Sceloporus gadowae
Eumeces altamirani
Cnemidophorus calidipes
Cnemidophorus costatus
Hypsiglena torquata
Leptodeira latifasciata
Pseudoficimia frontalis
Sonora michoacanensis
Trimorphodon latifascia
Thamnophis dorsalis
Miscrurus distans

Fewer species reach the lower limits of their distributions primarily between 800 and 1000 meters. These are species that mainly inhabit the pine-oak forests and also occur in the higher parts of the tropical semi-deciduous forest; among species in this group are *Rana pustulosa, Leptodeira splendida, Leptophis diplotropis,* and *Rhadinaea hesperia.*

Next to the group of 53 species reaching their lower limits of distribution at or near sea level, the largest group contains 33 species reaching their lower altitudinal limits between 1400 and 1600 meters. Included in this group are species that are typical inhabitants of pine forest, such as:

Pseudoeurycea belli
Scaphiopus hammondi
Microbatrachylus hobartsmithi
Tomodactylus angustidigitorum
Tomodactylus rufescens
Hyla bistincta
Sceloporus grammicus
Eumeces dugesi
Gerrhonotus imbricatus
Conopsis biserialis
Toluca lineata
Storeria storerioides
Crotalus molossus
Crotalus pusillus

Also included in this group are species inhabiting the Mexican Plateau, which in Michoacán descends to an elevation of about 1500 meters. Plateau inhabitants reaching the lower limits of their distributions at this elevation include:

Bufo compactilis
Hypopachus oxyrrhinus
Rana megapoda
Rana montezumae
Kinosternon hirtipes
Sceloporus spinosus
Cnemidophorus scalaris
Masticophis taeniatus
Trimorphodon tau
Thamnophis melanogaster
Crotalus polystictus

A small group of species reach the lower limits of their distributions at about 1900 meters; most of these are species that inhabit the cool montane forests, such as *Ambystoma tigrinum, Tomodactylus fuscus, Sceloporus bulleri, Conopsis nasus, Diadophis dugesi,* and *Tantilla bocourti.*

Pseudoeurycea robertsi, which insofar as is known is restricted to the fir forest, reaches its lower limits at 2900 meters. All other species in the state occur at lower elevations.

The upper limits of distribution of nine species are at about 100 meters; these species are restricted to the coastal plain and include:

Rhinophrynus dorsalis
Phrynohyas inflata
Crocodylus acutus
Anolis schmidti
Dryadophis melanolomus
Geagras redimitus
Manolepis putnami
Natrix valida

The small group of species having their upper altitudinal limits between 300 and 500 meters are mostly those inhabiting only the lower parts of the Balsas-Tepalcatepec Basin and include:

Diaglena reticulata
Phyllodactylus duellmani
Enyaliosaurus clarki
Pseudoficimia pulcherrima
Tantilla calamaria
Micrurus distans

The upper limits of altitudinal distribution for the greatest number of species (35) is between 900 and 1100 meters, where the arid tropical scrub forest of lower elevations is replaced at higher elevations by pine-oak forest. Typical of the species that characteristically inhabit the lowlands and reach the upper limits of distribution at this altitude are:

Bufo marinus
Leptodactylus melanonotus
Phyllomedusa dacnicolor
Hyla smithi
Phyllodactylus lanei
Ctenosaura pectinata
Sceloporus pyrocephalus
Mabuya brachypoda
Ameiva undulata
Cnemidophorus communis
Cnemidophorus deppei
Heloderma horridum
Boa constrictor
Drymobius margaritiferus
Leptodeira maculata
Salvadora mexicana
Trimorphodon biscutatus

Ten species reach the upper limits of their distributions at about 1600 meters; most of these species inhabit the lowlands and invade the lower parts

of the Mexican Plateau. Included in this group are *Tomodactylus nitidus, Hyla smaragdina, Hypopachus caprimimus, Urosaurus bicarinatus,* and *Masticophis striolatus.* Another group of species reaches the upper limits of their distributions at about 2200 meters. Most of these are inhabitants of the Mexican Plateau; included in this group are:

Ambystoma tigrinum
Hypopachus oxyrrhinus
Rana montezumae
Kinosternon hirtipes
Sceloporus dugesi
Sceloporus scalaris
Lampropeltis ruthveni
Pituophis deppei
Trimorphodon tau
Thamnophis eques
Thamnophis melanogaster

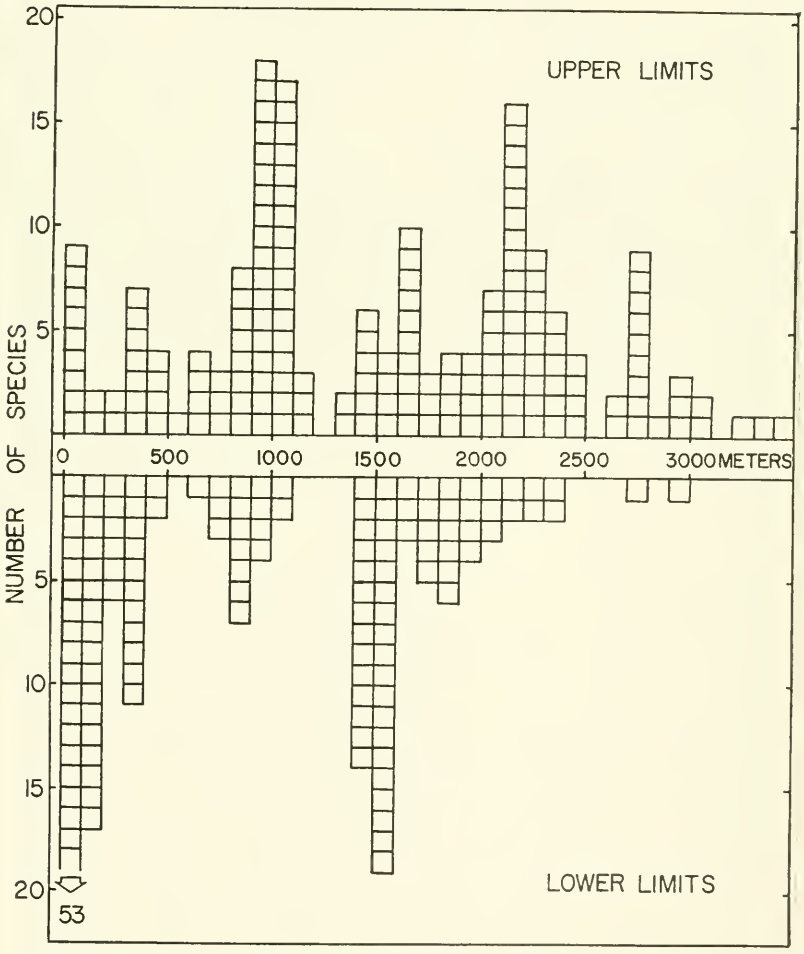


FIG. 4. Numbers of species of amphibians and reptiles reaching their upper and lower altitudinal limits at various elevations in Michoacán.

The group of species apparently reaching the upper limits of their distributions at about 2800 meters possibly is the result of inadequate collecting, rather than actual upper limits of distribution, for few areas above this elevation have been studied thoroughly. Eight species are known to occur at elevations of 3000 meters or more. Two of these are amphibians—*Ambystoma ordinarium* and *Pseudoeurycea robertsi;* both inhabit the fir forest. The six reptiles inhabiting the highest elevations are *Sceloporus torquatus* (3000 m.), *Scleoporus aeneus* (3100 m.), *Sceloporus grammicus* (3100 m.), *Crotalus triseriatus* (3270 m.), *Thamnophis scalaris* (3400 m.), and *Gerrhonotus imbricatus* (3500 m.).

Factors Affecting Distribution

Within the various vegetation types discussed previously and within the altitudinal limits set forth above, each species possesses certain characters that enable it to survive under a given set of environmental conditions and probably preclude its occurrence in other habitats. Little is known of ecological tolerances of the species of amphibians and reptiles inhabiting Michoacán, so interpretations of ecological factors that seem to restrict the distributions of species must be made on the basis of observations in the field. Some species obviously are closely associated with certain ecological conditions that can be observed readily; for example, *Cnemidophorus calidipes* is always found in the *Acacia-Cercidium-Prosopis* association in the Tepalcatepec Valley. Although *Acacia* and *Prosopis* are widespread in the lowlands, *Cnemidophorus calidipes* occurs only in that part of the scrub forest where *Cercidium* grows. What the ecological relationships are remains to be discovered, but the distributional limits of *Cnemidophorus calidipes* are obvious.

Analysis of distributional data and ecological data shows that several ecological factors seem to limit the distributions of some species either within a major habitat or within the entire region. The factors that I think important are discussed below.

Microhabitats

Subdivisions can be recognized within each of the five major habitats in Michoacán. For most of the species under consideration the recognition of five microhabitats is sufficient—arboreal, terrestrial, fossorial, riparian, and aquatic. Some of these could be divided further; for example, in the arboreal habitat it is possible to discern species that inhabit tree trunks and others that inhabit branches. However, such refinement is unnecessary to demonstrate the effects of the presence or absence of certain microhabitats in a given habitat on the distribution of amphibians and reptiles. The distribution of the numbers of species by microhabitats in the major habitats is shown in Table 3.

Although the arboreal microhabitat is well developed in the tropical semideciduous forest, the pine-oak forest, and the fir forest, a much higher percentage of species is arboreal in the tropical semi-deciduous forest. In that habitat *Phyllomedusa dacnicolor, Sceloporus melanorhinus, Leptophis diplotropis,* and *Oxybelis aeneus* are abundant arboreal species. Five of the ten arboreal species in the pine-oak forest and all three of the arboreal species in the fir forest are species of *Sceloporus.* Other arboreal species in the pine-oak forest are lowlanders that extend into the lower altitudinal range of the pine-oak forest; these include *Anolis nebulosus, Leptophis diplotropis,* and *Oxybelis*

TABLE 3.—COMPARISON OF ACTUAL AND RELATIVE NUMBERS OF SPECIES OF AMPHIBIANS AND REPTILES FOUND IN VARIOUS MICROHABITATS IN THE MAJOR HABITATS IN MICHOACÁN.

MICROHABITAT	Arid tropical scrub forest	Semi-deciduous tropical forest	Mesquite-grassland	Pine-oak forest	Fir forest
Arboreal	7 (9.2%)	15 (24.6%)	2 (5.1%)	10 (14.3%)	3 (13.0%)
Terrestrial	53 (69.7%)	32 (52.4%)	28 (71.8%)	35 (50.0%)	9 (39.0%)
Fossorial	7 (9.2%)	6 (9.8%)	1 (2.5%)	18 (25.7%)	9 (39.0%)
Riparian	6 (7.9%)	7 (11.6%)	6 (15.6%)	5 (7.0%)	2 (9.0%)
Aquatic	3 (4.0%)	1 (1.6%)	2 (5.0%)	2 (3.0%)	0 (0.0%)

aeneus. The lack of cover due to deciduousness apparently precludes or greatly restricts the habitation of the scrubby trees in the arid tropical scrub forest by most of the species living in the tropical semi-deciduous forest. Although nine species are partly arboreal in the arid tropical scrub forest, only *Urosaurus gadowi*, which lives on the trunks of small trees, *Enyaliosaurus clarki*, which lives on the branches of trees and takes refuge in hollow branches, and *Phyllodactylus duellmani*, which lives in the columnar cacti and standing dead trees, are primarily arboreal. In the mesquite-grassland on the Mexican Plateau, the arboreal habitat is poorly represented. Only two species there are partly arboreal; *Hyla smaragdina* inhabits bromeliads on small trees, and *Anolis nebulosus* sleeps at night on low bushes.

Terrestrial species, as classified here, include those that live on the ground but do not characteristically burrow or inhabit the mulch layer. Excluded from this category are species that normally inhabit the edges of streams, ponds, or other bodies of water thoughout the year. In the fir forest 39 per cent of the amphibians and reptiles are terrestrial, but in the other habitats at least 50 per cent of the species live on the ground. The highest percentage of terrestrial species is in the open habitats—arid tropical scrub forest and mesquite-grassland. The small amount of vegetational cover and near absence of mulch in these habitats is correlated with the presence of many fast and agile species there: *Masticophis striolatus, M. taeniatus, Salvadora bairdi, S. mexicana*, and several species of *Cnemidophorus* are characteristic. Many terrestrial species inhabit rocky areas, often natural outcrops or rock fences. In the arid tropical scrub forest *Ctenosaura pectinata, Sceloporus gadowae, S. horridus*, and *S. pyrocephalus* are common saxicolous species. In the mesquite-grassland *S. dugesi* and *S. spinosus* are among the conspicuous inhabitants of rock fences.

Included as fossorial species are those that burrow or inhabit the mulch on the forest floor. Few fossorial species are known from the arid tropical scrub forest and mesquite-grassland, where a layer of mulch is almost non-existent. Although mulch is present in the tropical semi-deciduous forest, only a few species live in it, such as *Scincella assata, Leptotyphlops phenops, Enulius unicolor, Geagras redimitus*, and *Rhadinaea hesperia*. In the cooler pine-oak and

fir forests the mulch is well developed, and in these habitats many species live in the mulch. Characteristic inhabitants of the mulch are salamanders of the genera *Ambystoma* and *Pseudoeurycea,* lizards of the genus *Eumeces,* and snakes of the genera *Conopsis, Diadophis, Geophis, Rhadinaea, Tantilla,* and *Toluca.* Mulch apparently is a positive factor responsible for the distributions of many of these animals.

Water, either in permanent ponds or flowing streams, is an important factor in the distributions of many species. Species characteristically found near water throughout the year are grouped into two categories—riparian and aquatic. The riparian inhabitants include various species of *Rana* and *Thamnophis* that live around the lakes and marshes on the Mexican Plateau. They make up 15 per cent of the herpetofauna of the mesquite-grassland. Also in this group are frogs, such as *Eleutherodactylus rugulosus, Hyla arenicolor, Hyla bistincta,* and *Rana pustulosa,* which always are found along streams, and the lizards *Basiliscus vittatus* and *Iguana iguana,* which live at the edge of permanent bodies of water. Aquatic members of the herpetofauna include the salamanders of the genus *Ambystoma.* (*Ambystoma dumerili* is known only from neotenic individuals, and some populations of the other species of *Ambystoma* are neotenic.) Turtles and the crocodile make up the rest of the aquatic herpetofauna. The majority of the aquatic species live in lakes or lagoons, but *Kinosternon integrum* lives also in quiet streams, and neotenic individuals of *Ambystoma ordinarium* also inhabit streams. Streams having steep gradients are important microhabitats for *Hyla arenicolor* and *Rana pustulosa,* but these same streams are barriers to the distribution of inhabitants of quiet water, such as *Kinosternon integrum.*

Reproductive Habits

Diversity of reproductive habits among amphibians and reptiles indicates a variety of factors necessary for the species to maintain populations in a given environment. Although detailed information on the life histories is available for only a few species, data concerning sites of egg deposition and oviparity *versus* ovoviviparity are available. Analysis of these data provides evidence that the availability of suitable breeding sites and the methods of producing young importantly affects the ecological distributions of many species.

Since the modes of reproduction in amphibians differ from those of reptiles, the two groups will be considered separately. Some amphibians utilize a variety of breeding sites; usually such species are widespread ecologically and geographically. For example, *Rana pipiens,* the most widespread amphibian in Michoacán and the only species that lives in all five major habitats, breeds and deposits its eggs in almost any aquatic situation except fast-moving streams. Other species are more restricted as to their breeding sites; *Hyla bistincta* deposits its eggs only in fast-moving mountain streams, and *Phyllomedusa dacnicolor* suspends its eggs from bushes and trees over shallow ponds. The eggs of two plethodontid salamanders of the genus *Pseudoeurycea* and of nine species of leptodactylid frogs of the genera *Eleutherodactylus, Microbatrachylus,* and *Tomodactylus* develop on land. Habitats in which the layer of mulch is well developed provide favorable sites for deposition of eggs. In the pine-oak forests, eight species (40 per cent of the amphibians living in that habitat) lay their eggs in the well-developed layer of mulch, whereas in the arid tropical scrub forest, where the mulch layer is poorly developed, only

two species (8.7%) lay terrestrial eggs. The abundance of streams varies in different habitats; in the mesquite-grassland on the Mexican Plateau, only one species of amphibian breeds in the streams, most of which are intermittent, but in the pine-oak forest and tropical semi-deciduous forest, where small streams are numerous, six species of amphibians deposit their eggs in streams. The correlation between egg deposition sites and major habitats is shown in Table 4.

TABLE 4.—COMPARISON OF ACTUAL AND RELATIVE NUMBERS OF SPECIES OF AMPHIBIANS THAT USE VARIOUS EGG DEPOSITION SITES IN THE MAJOR HABITATS IN MICHOACÁN.

DEPOSITION SITE	Arid tropical scrub forest	Semi-deciduous tropical forest	Mesquite-grassland	Pine-oak forest	Fir forest
Temporary Pond...	14 (60.8%)	8 (36.4%)	7 (50.0%)	4 (20.0%)	2 (28.5%)
Permanent Pond...	2 (8.7%)	2 (9.1%)	4 (28.6%)	2 (10.0%)	1 (14.3%)
Stream.....	4 (17.4%)	6 (27.2%)	1 (7.1%)	6 (30.0%)	3 (42.9%)
Terrestrial.....	2 (8.7%)	5 (22.7%)	2 (14.3%)	8 (40.0%)	1 (14.3%)
Arboreal/Pond.....	1 (4.4%)	1 (4.6%)	0 (0.0%)	0 (0.0%)	0 (0.0%)

Most reptiles lay eggs, but some lizards and snakes give birth to young. Although information concerning the reproductive habits is lacking for some species, data are available for enough species to draw some conclusions about the reproductive habits as they relate to distribution. Most species of snakes and lizards in the lowlands below an elevation of 1000 meters are oviparous and deposit their eggs in rotting logs and stumps, in mulch, in loose soil, or beneath stones. Solar radiation and the continuously warm substrate provide sufficient heat for incubation. At successively higher elevations the percentage of oviparous species decreases. Six species of reptiles (*Sceloporus grammicus*, *S. aeneus*, *S. torquatus*, *Gerrhonotus imbricatus*, *Thamnophis scalaris*, and *Crotalis triseriatus*) occur at elevations in excess of 3000 meters; all are ovoviviparous. The activities of these animals are restricted to the warm parts of days in a relatively short summer. Apparently the habit of basking in the sunshine provides sufficient warming of the body to allow development of the eggs in the females, whereas eggs laid in the continuously cool mulch or soil would not receive sufficient heat to develop. The correlation between ovoviviparity and altitude parallels that between ovoviviparity and northward extent of range of some species, such as *Gerrhonotus multicarinatus* and *Thamnophis sirtalis* in North America and *Lacerta vivipera* and *Vipera berus* in Eurasia.

Diel Activity

Conditions in the various major habitats and included microhabitats control the diel activities of the amphibians and reptiles living there. Throughout Michoacán most amphibians are nocturnal. The low intensity of light on the

floor of the tropical semi-deciduous forest, combined with the relatively high humidity and moist layer of mulch, provides conditions favorable for the diurnal activities of some small amphibans, such as *Eleutherodactylus occidentalis* and *Microbatrachylus pygmaeus*. Other amphibians, such as *Eleutherodactylus rugulosus*, *Hyla arenicolor*, and *Rana pustulosa*, inhabit stream beds in ravines, where the amount of light is reduced in the daytime; consequently, these species often are diurnal.

The crocodile and the turtles of the genus *Kinosternon* are sometimes active by day but are chiefly nocturnal.

Lizards and snakes are characterized by a wide range of diel activity. Most lizards are diurnal; in Michoacán geckos of the genus *Phyllodactylus* are an exception. In the arid tropical scrub forest few reptiles are active during the hottest part of the day when temperatures at mid-day sometimes exceed 43° C. *Cnemidophorus calidipes* is a notable-exception. Most active terrestrial species, such as *Drymobius margaritiferus*, *Masticophis striolatus*, *Salvadora mexicana*, *Sceloporus pyrocephalus*, *S. siniferus*, and the various species of *Cnemidophorus*, have two daily peaks of activity, the early daylight hours until about 10 AM and the late afternoon from about 5 PM until dusk. In the mesquite-grassland on the Mexican Plateau, where temperatures at mid-day are moderate, distinct morning and late afternoon periods of activity are lacking; instead, most diurnal species are active throughout the day. In the tropical semi-deciduous forest, where dense foliage provides shade, agile species, such as *Ameiva undulata*, *Cnemidophorus lineatissimus*, *Dryadophis melanolomus*, *Leptophis diplotropis*, and *Oxybelis aeneus*, are active throughout the day.

Increase in altitude is correlated with decrease in duration of diurnal activity, at least in the lizards of the genus *Sceloporus*. At Uruapan at an elevation of 1630 meters, *Sceloporus grammicus* and *S. torquatus* often were active before 8 AM, but at Mil Cumbres at an elevation of 2800 meters, these lizards were not seen before 10 AM, and then only on clear days.

In the arid tropical scrub forest, where nocturnal temperatures are moderate relative to the diurnal temperatures, more than 50 per cent of the lizards and snakes are nocturnal (Table 5). In the hot Balsas-Tepalcatepec Basin some species, such as *Drymarchon corais*, are nocturnal, whereas in other parts of their ranges they normally are diurnal. In the mesquite-grassland and pine-oak forest *Thamnophis dorsalis* is diurnal, but in the Tepalcatepec Valley is nocturnal. Many of the small mulch-inhabiting snakes, such as *Conopsis* and *Geophis*, in the pine-oak forest apparently are nocturnal. Lower nocturnal temperatures on the Mexican Plateau apparently restrict nocturnal activity there; only *Elaphe triaspis*, *Thamnophis melanogaster*, and *Trimorphodon tau* commonly are found at night.

Possibly the low nocturnal temperature limits the altitudinal distribution of such strictly nocturnal animals as lizards of the genus *Phyllodactylus* and snakes of the genus *Leptodeira*. Likewise, the excessive heat and light in the arid tropical scrub forest possibly precludes the occupation of that habitat by lizards such as *Ameiva undulata* and *Cnemidophorus lineatissimus*, both of which live in the adjacent tropical semi-deciduous forest. An adequate understanding of the significance of diel activity as related to distribution must await data from detailed studies of temperature responses of the species concerned.

TABLE 5.—COMPARISON OF ACTUAL AND RELATIVE NUMBERS OF SPECIES OF LIZARDS AND SNAKES HAVING NOCTURNAL AND DIURNAL HABITS IN THE VARIOUS MAJOR HABITATS IN MICHOACÁN.

PERIOD OF ACTIVITY	Arid tropical scrub forest	Semi-deciduous tropical forest	Mesquite-grassland	Pine-oak forest	Fir forest
Diurnal.....	25 (47.2%)	29 (65.9%)	17 (70.8%)	31 (67.4%)	10 (71.4%)
Nocturnal.....	28 (52.8%)	15 (34.1%)	7 (29.2%)	15 (32.6%)	4 (28.6%)

Ecological Segregation

Similar adaptations and requirements in closely related species affect the distributions of some species within and between communities. Many observations in nature, as well as experimental evidence, have demonstrated that two or more species having closely similar niche-requirements cannot exist as stabilized populations in the same area; this concept, which has been known as Gause's Rule, was thoroughly discussed and defined as the "Competitive Exclusion Principle" by Hardin (1960). Observations in the field indicate that in Michoacán several species-pairs seem to have closely similar niche-requirements. Members of each of these pairs are segregated geographically. For example, *Sceloporus bulleri* and *S. torquatus* closely resemble each other morphologically, and each inhabits pine and fir forests, where both live on the ground and on the trunks of the large trees, but the former species occurs in the Sierra de Coalcomán and the latter in the Cordillera Volcánica. Although these two species are segregated geographically, each occurs sympatrically with other species of *Sceloporus*, which, because of differences in morphology or habits, have different niche-requirements.

Data to support concepts of ecological segregation of animals in nature are difficult to obtain, especially on amphibians and reptiles, many of which are secretive in their habits. The abundant and conspicuous iguanids, *Sceloporus* and *Urosaurus*, are notable exceptions. In a transect from the Mexican Plateau, over the Cordillera Volcánica, down to the Tepalcatepec Valley, 12 species of *Sceloporus* and one of *Urosaurus* can be found. Three or more species occur in each of the five major habitats included in the transect. Sympatric species differ in size or in their microhabitats. On the Mexican Plateau two species are broadly sympatric, and each is terrestrial and saxicolous; of these, *S. spinosus* is large, and *S. dugesi* is small. Another small species, *S. scalaris*, is restricted to bunch-grass associations on the plateau and in the Cordillera Volcánica. In the coniferous forests on the Cordillera Volcánica there are two small species—the terrestrial *S. aeneus* and the arboreal *S. grammicus*. Also living there is the large *S. torquatus*, which lives on the ground and on trees. At an elevation of about 1000 meters on the slopes of the Cordillera Volcánica the highland species of *Sceloporus* are replaced in the broad-leafed oak or tropical semi-deciduous forest by an assemblage of lowland species, of which *S. asper* is small and arboreal, *S. melanorhinus* is large and arboreal, and *S. utiformis* is terrestrial. At lower elevations in the

arid tropical scrub forest *S. melanorhinus* is still the large arboreal species, but *Urosaurus gadowi* has replaced *S. asper* as the small arboreal species. The terrestrial species include the large *S. horridus* and the small *S. pyrocephalus*. On conglomerate cliffs the latter species is replaced by *S. gadowae*.

In another transect, one from the high ridges of the Sierra de Coalcomán to the Pacific coast, many of the species found in the lowlands are the same as those listed in the previously described transect, but some additional species are present on the Pacific coastal lowlands. Entirely different species of lizards occur in the two highland areas. In the coniferous forest in the Sierra de Coalcomán the small arboreal *Sceloporus heterolepis* is the ecological equivalent of *S. grammicus* in the Cordillera Volcánica. *Sceloporus bulleri*, which lives on the ground and on the trees in the Sierra de Coalcomán, is the ecological equivalent of *S. torquatus* in the Cordillera Volcánica. The niche filled by *S. aeneus* in the Cordillera Volcánica apparently is vacant in the Sierra de Coalcomán. In the tropical semi-deciduous forest on the seaward slopes of the Sierra de Coalcomán only two species of *Sceloporus* occur —the large arboreal *S. melanorhinus* and the terrestrial *S. utiformis*. In the arid tropical scrub forest on the Pacific lowlands *S. melanorhinus* is the large arboreal species, *Urosaurus bicarinatus* is the small arboreal species, and *S. horridus* is the large terrestrial species. In rocky areas in the Pacific lowlands *S. pyrocephalus* is the small terrestrial species, but in open areas there it is replaced by *S. siniferus*.

Similar selection of microhabitats that apparently allow several related species to live in a single community has been demonstrated in other groups of animals, for example, lizards of the genus *Anolis* (Duellman, 1963). Direct competition between arboreal and terrestrial species obviously is slight, but competition may exist between two arboreal, or between two terrestrial, species in a given community. The distinct difference in size between species such as *Sceloporus grammicus* and *S. torquatus*, which is about twice the length and about five times the bulk of the former, suggests that, at least for adults, food items probably differ. However, juveniles of *S. torquatus* may consume the same kinds of food as does *S. grammicus*, at which time the two species may be in direct competition. Studies on the autecology of these lizards are needed to clarify their ecological interrelationships.

Differences in size in sympatric pairs of species have been noted in *Chiropterotriton* by Rabb (1958) and in *Cnemidophorus* by Zweifel (1960) and Duellman (1960a). Additional evidence on sizes of ecological pairs of teiid lizards of the genera *Ameiva* and *Cnemidophorus* supports observations on ecological segregation in these lizards. In certain areas in the Tepalcatepec Valley five species of *Cnemidophorus* and one species of *Ameiva* are sympatric. *Ameiva undulata* and the smaller *Cnemidophorus lineatissimus* are widespread in the tropical semi-deciduous forest on the seaward slopes of the Sierra de Coalcomán, but in the Tepcalcatepec Valley these species occur only on the shady floor of the gallery forest along major streams. In the ecotone between the gallery forest and the arid tropical scrub forest *A. undulata* and *C. lineatissimus* are sometimes found with other species of *Cnemidophorus*—two large species (*C. communis* and *C. costatus*) and two small species (*C. calidipes* and *C. deppei*). Although both of the small species live in open areas in the arid tropical scrub forest in the Tepalcatepec Valley, each has noticeable ecological preferences. *Cnemidophorus deppei* is most abundant in open grassy areas, especially in arroyos where the vegetation is more lush than

on the adjacent flats, where *C. calidipes* lives on nearly barren ground supporting only sparse stands of grass below the scattered scrubby trees. The ecological segregation between *C. communis* and *C. costatus* is not so well marked. *Cnemidophorus costatus* is abundant throughout the Tepalcatepec Valley and is closely associated with both *C. calidipes* and *C. deppei*, but does not occur on the coastal lowlands. *Cnemidophorus communis* is uncommon and only locally present in the Tepalcatepec Valley, is more abundant on the coastal lowlands, and is the only species of *Cnemidophorus* in some of the valleys in the Sierra de Coalcomán. Probably *C. communis* is a recent invader in the Tepalcatepec Valley, where it may be in direct competition with *C. costatus*.

Other ecological species pairs or equivalents are present in Michoacán. In the Tepalcatepec Valley *Bufo perplexus* replaces *Bufo marmoreus*, which is restricted to the coastal lowlands. In the Sierra de Coalcomán *Geophis nigrocinctus* and *G. incomptus* replace *G. tarascae* and *G. maculiferus* of the Cordillera Volcánica. On the Mexican Plateau *Hypopachus oxyrrhinus*, *Masticophis taeniatus*, and *Salvadora bairdi* are the respective ecological equivalents of *Hypopachus caprimimus*, *Masticophis striolatus*, and *Salvadora mexicana* in the Tepalcatepec Valley.

The meager data on ecological segregation and replacement indicate that in well-known groups the species are segregated ecologically within major habitats, and that in ecotones between major habitats the species comprising a community in one habitat are replaced by another group of species in the second habitat. Interspecific competition may be significant in maintaining distributional limits in a climax environment and in effecting dispersal in areas of ecological succession.

Influence of Man

Much of Michoacán has been inhabited by man since pre-historic times. Ancient Aztecs and Tarascans cultivated extensive areas on the Mexican Plateau. Pine forests in the Cordillera Volcánica were cut to provide fuel for the perpetual fires that were a part of Tarascan religion. Probably the amount of cultivation and cutting by means of crude indian implements was slight in comparison with that accomplished by use of the iron plows and axes introduced by the Spaniards in the Sixteenth Century. Now, these tools seem crude as compared with modern mechanized equipment.

Obviously man has altered habitats in many areas in Michoacán. Marshes on the Mexican Plateau have been partly drained; lakes and irrigation ditches have been created in the lowlands. Many forested areas have been cleared, and over-grazing probably has altered the mesquite-grassland on the Mexican Plateau. Agricultural malpractices have resulted in widespread erosion, and irrigation probably has modified the level of the water table in some areas.

There is no evidence that any major habitat has been eliminated by man in any physiographic area, but some habitats have been partly altered or reduced in area. Constriction of one habitat results in the expansion of an adjacent habitat or the creation of a new habitat, and the distributions of some species have been altered accordingly. In other instances the habitats of some species probably have been modified, but with minor adjustments the species are able to survive in them. Among the probably more important results of

human alteration of natural habitats in Michoacán are the following: change in vegetation on the Mexican Plateau from grasses and mesquite to a legume-cacti-agave association due to over-grazing, formation of pine savannas having little or no understory due to heavy grazing by goats, reduction of forested areas because of lumbering, reduction of marshes by draining, creation of aquatic and aquatic margin microhabitats in arid areas through irrigation, and creation of an extensive network of microhabitat for saxicolous species by the construction of rock fences. The patterns of ecological and geographical distribution probably have not been altered significantly by man.

Analysis of Ecological Distribution

The ecological distribution of amphibians and reptiles in Michoacán is closely correlated with the limits of the major types of vegetation or animal habitats as defined previously on page 641. Of the 183 species and subspecies analyzed, 115 (62.8%) are restricted to one habitat; 55 (30%) occur in only two habitats, whereas only seven (3.8%) occur in three habitats, five (2.8%) in four habitats, and one species (0.6%) in all five habitats. The number of species that occupy more than one habitat decreases as the habitats become more diverse. For example, of the 77 species inhabiting the arid tropical scrub forest, 26 also live in the tropical semi-deciduous forest, ten in the mesquite grassland, nine in the pine-oak forest, and only one in the fir forest. Of the

TABLE 6.—ANALYSIS OF DISTRIBUTIONS OF AMPHIBIANS AND REPTILES BY MAJOR TAXONOMIC GROUPS IN THE MAJOR HABITATS IN MICHOACÁN. (Percentages are the proportion of the taxonomic group in a given habitat. Numbers in parentheses after the name of the group indicate the number of species and subspecies belonging to that group in Michoacán.)

GROUP	Arid tropical scrub forest	Tropical semi-deciduous forest	Mesquite-grassland	Pine-oak forest	Fir forest
Salamanders (6)....	0 0.0%	0 0.0%	0 0.0%	5 83.3%	4 66.8%
Frogs and toads (42)	18 42.9%	17 40.5%	13 30.9%	18 42.9%	5 11.9%
Turtles (5).....	4 80.0%	1 20.0%	2 40.0%	1 20.0%	0 0.0%
Crocodilians (1)....	1 100.0%	0 0.0%	0 0.0%	0 0.0%	0 0.0%
Lizards (52).....	22 42.3%	21 40.4%	7 13.5%	17 32.6%	7 13.5%
Snakes (77).....	32 41.6%	23 29.9%	17 22.1%	29 37.7%	7 9.1%
Total species per habitat.....	77 42.1%	62 39.4%	39 21.3%	70 38.3%	23 13.7%

62 species inhabiting the tropical semi-deciduous forest, 17 also live in the pine-oak forest, eight in the mesquite-grassland, and only one in the fir forest. Of the 39 species inhabiting the mesquite-grassland, 19 also live in the pine-oak forest, and three in the fir forest. The largest amount of ecological interchange is between the fir forest and the pine-oak forest; of the 23 inhabitants of the fir forest, 22 are among the 70 species that occur in the pine-oak forest.

TABLE 7.—ACTUAL AND RELATIVE NUMBERS OF SPECIES AND SUBSPECIES OF MAJOR GROUPS OF AMPHIBIANS AND REPTILES LIVING IN VARIOUS HABITATS IN MICHOACÁN. (Percentages are the proportion of the total herpetofauna in a habitat comprised by the taxonomic group. Numbers in parentheses after the name indicate the number of species and subspecies belonging to that group in Michoacán.)

GROUP	Arid tropical scrub forest	Tropical semi-deciduous forest	Mesquite-grassland	Pine-oak forest	Fir forest
Salamanders (6)....	0 0.0%	0 0.0%	0 0.0%	5 7.1%	4 17.4%
Frogs and toads (42)	18 23.4%	17 27.4%	13 33.3%	18 25.7%	5 21.8%
Turtles (5).....	4 5.2%	1 1.6%	2 5.1%	1 1.4%	0 0.0%
Crocodilians (1)....	1 1.3%	0 0.0%	0 0.0%	0 0.0%	0 0.0%
Lizards (52).....	22 28.6%	21 33.9%	7 18.0%	17 24.4%	7 30.4%
Snakes (77).....	32 41.5%	23 37.1%	17 43.6%	29 41.4%	7 30.4%
Total (183).....	77 100.0%	62 100.0%	39 100.0%	70 100.0%	23 100.0%

As expected, the ecological distributions of the major taxonomic groups of amphibians and reptiles differ. In Table 6 the ecological distributions are analyzed on the basis of the groups. For example, in Michoacán only one crocodilian occurs. It lives in the lagoons in the arid tropical scrub forest; thus, one hundred per cent of the crocodilian fauna occurs in that habitat. In Table 7 the distributions are analyzed on the basis of habitats. In this analysis the one crocodilian inhabiting the arid tropical scrub forest accounts for only 1.3 per cent of the species of amphibians and reptiles in that habitat. Salamanders are absent in the tropical habitats, but frogs are about equally distributed in the arid tropical scrub forest, tropical semi-deciduous forest, and pine-oak forest. Lizards are about equally diverse in the two tropical habitats, but there are fewer species in the pine-oak forest and far fewer species in the mesquite-grassland and fir forest. The species of snakes are nearly as numerous in the pine-oak forest as in the arid tropical scrub forest; fewer species occur

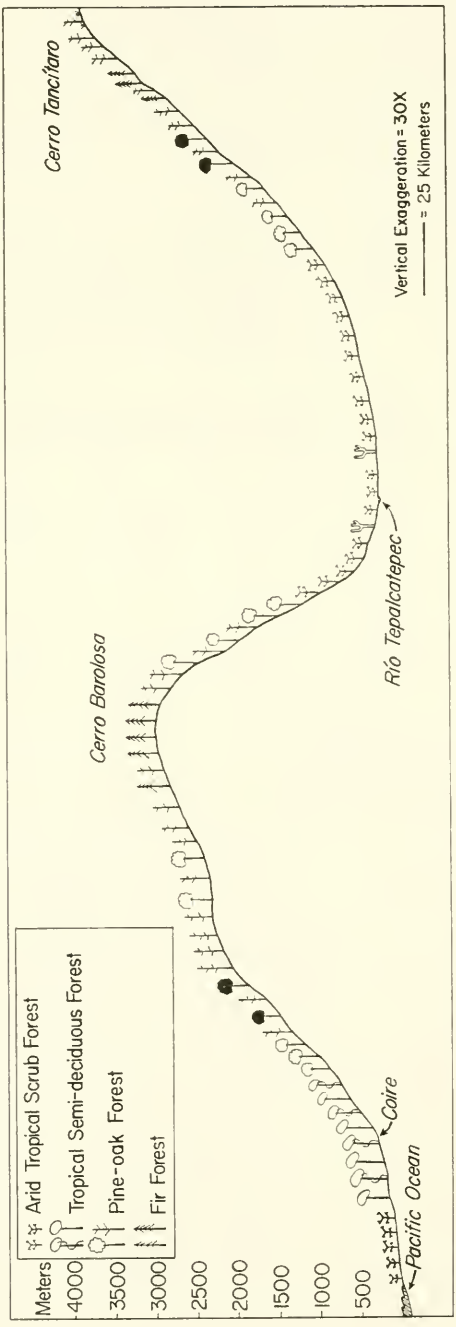


FIG. 5. Profile of southern Michoacán from Cerro Tancítaro to the Pacific Ocean showing distribution of major habitats. The solid symbols indicate areas in which a cloud forest type of vegetation occurs.

in the tropical semi-deciduous forest and in the mesquite-grassland, and far fewer live in the fir forest.

The good correlation between distributions of the components of the herpetofauna and the habitats suggests that the definition of habitats proposed here is real in that it rather accurately reflects the ecological factors that are significant in limiting the distributions of most of the species. The analysis of altitudinal distribution shows that most species reach the upper or lower limits of their distributions at elevations approximating the altitudinal limits of the major habitats. It should be noted that the altitudinal limits of the habitats vary from windward to leeward slopes and differ in the Cordillera Volcánica from those in the Sierra de Coalcomán (Fig. 5). These variations account, in part, for some of the discrepancies in altitudinal distributions of the amphibians and reptiles.

In some aquatic species and others inhabiting microhabitats that are not directly dependent on a given kind of vegetation, the overall ecological distributions are not well correlated with the limits of the major habitats. Nevertheless, the physiognomy of the vegetation and resulting microhabitats seem to be the most important factors in determining the ecological distributions of amphibians and reptiles in Michoacán.

GEOGRAPHY OF THE HERPETOFAUNA

The geographical analysis presented here is centered on the herpetofauna of Michoacán but applies to the herpetofauna of a large part of southwestern México. An attempt is made to answer four questions.—1.) How can the geographical relationships of the various faunal assemblages in southwestern México best be described and analyzed? 2.) What is the distribution of each of the species of amphibians and reptiles in Michoacán and adjacent areas? 3.) What are the patterns of distribution of amphibians and reptiles in southwestern México? 4.) How are these patterns related to one another and to the patterns in outlying regions?

Methods of Zoogeographic Analysis

Zoogeographers work with facts and inferences drawn from a variety of sources; in most cases no one set of data is complete. Consequently, many generalizations are arrived at by deductive extrapolation. Zoologists since Humboldt in the early Nineteenth Century have tried with various degrees of success to analyze regional (as opposed to world-wide) faunas.

Three methods of regional analysis have been used, and Kendeigh (1954) has reviewed their history and evaluated each. The oldest and first method utilizes the Life-zone Concept of Merriam (1890, 1894); although temperatures (isotherms) are the theoretical basis for this classification, in practice floristic indices are utilized. Life-zones are discontinuous areas. They have been used more satisfactorily in the mountainous regions of western North America, where floristic and temperature breaks are sharp, than in the eastern part of North American where gradual changes in elevation result in less sharp floristic, faunal, or climatic boundaries. Goldman (1951) applied the Life-zone Concept in his discussion of the distribution of vegetation, birds, and mammals in México, and he recognized six zones in Michoacán. According

to him, the Lower Tropical Life-zone is divided into the Humid Lower Tropical Subzone and the Arid Lower Tropical Subzone; the latter occurs on the Pacific Coastal Plain and slopes of adjacent mountains to elevations of about 2,500 feet and extends from Nayarit to Chiapas. The Upper Tropical Life-zone also is divided into two subzones, of which the Humid Upper Tropical Subzone corresponds to what I have defined as cloud forest in the earlier section on vegetation. This kind of forest does not occur in Michoacán, but cloud forest does occur in the Sierra Madre del Sur and possibly in the Sierra de Autlán in Jalisco. Goldman's Lower Austral Life-zone includes the slopes of the western Mexican highlands, whereas the Transition Life-zone includes most of the mountainous regions above 7,000 feet, and the Canadian Life-zone includes only the highest peaks, where fir forest occurs. Essentially this classification of Life-zones is nothing more than the application of names to habitats or vegetational formations. This aspect of the distribution of the herpetofauna in Michoacán already has been presented in the section on ecology of the herpetofauna. It is significant to note that the ecological distribution of a species does not necessarily reflect the geographical distribution of either the species or its Life-zone. The plotting of Life-zones and associated species of animals on the Pacific slopes of the Sierra de Coalcomán reveals the altitudinal distribution of environments and associated animals, but a similar transect on the slopes of the Sierra Madre del Sur in Guerrero or on the Sierra Madre Oriental in Veracruz shows the same Life-zones, but most species of animals inhabiting these Life-zones are different from those in Michoacán. Therefore, for understanding patterns of animal distribution on a spatial (horizontal) scale the Life-zone Concept is unsatisfactory.

The second method of faunal analysis is the Biotic Province Concept, which was proposed by Vestal (1914) and refined for North America by Dice (1943), who defined a biotic province as a considerable and continuous geographic area that is characterized by the occurrence of one or more important ecological associations that differ, at least in proportional area covered, from the associations of adjacent provinces. Theoretically, this concept has much in its favor, since it is based on principles of community ecology and finds its application in the common limits of distribution of biological taxa. Objectons to the concept of biotic provinces have been many. Johnson, Bryant, and Miller (1948), Miller (1951), and Kendeigh (1954) have pointed out difficulties in applying nebulous principles of community ecology to patterns of distribution and have emphasized the importance given to geographical boundaries instead of actual animal distributions. Smith (1939, 1940, and 1949) mapped the Biotic Provinces of México; his earlier works were based solely on the distribution of the species of *Sceloporus,* whereas the last paper was based on the distributions of all amphibians and reptiles. Moore (1945) similarly mapped the Biotic Provinces of México on the basis of avian distribution, and Goldman and Moore (1956) repeated the process for mammalian distribution. Although there is considerable agreement in the various maps, there are important differences.

The availability of neatly delimited regions drawn on maps seems to have contributed to the popularity of the Biotic Province Concept. This popularity has resulted in widespread use and misuse of the concept, especially by workers who were not familiar with the premises on which the concept is based. The establishment of a biotic province on distributions of a

few species (Firschein and Smith, 1956) and the establishment of a system of biotic provinces on the distribution of a limited taxonomic group of animals (Smith, 1939, 1940, and Stuart, 1943) are unwarranted. Equally misleading are descriptions of geographic distributions of species on the basis of biotic provinces, when the actual known range of the species includes only a small part of the biotic province. Peters (1955) discussed various uses and misuses of the Biotic Province Concept, especially as it has been applied to southwestern México. Biotic provinces are best applied on a horizontal scale; in mountainous regions the biotic provinces have little use. Smith, an early proponent of the Biotic Province Concept, recently (1960) registered his disillusionment and suggested disregarding the concept. Axtell (1962) argued for the use of the concept and suggested the inclusion of an "endemism clause," which would seem further to complicate the usefulness of the concept. According to Goldman and Moore (1946), the Sierra de Coalcomán and all of the lowlands in Michoacán are part of the Nayarit-Guerrero Province extending along the Pacific coast from Nayarit to Guerrero, and all of the rest of the state is contained in the Transverse Volcanic Province, which extends from Nayarit and Jalisco to Veracruz. According to Smith (1949), the coastal lowlands and the Sierra de Coalcomán are part of the Acapulcan Province, which consists of the southern coastal part of Goldman and Moore's Nayarit-Guerrero Province. Smith placed the Balsas Basin in a separate Balsan Province, the Cordillera Volcánica as part of the Austro-Occidental Province, and the Mexican Plateau in the Austro-Central Province. The lack of agreement on boundaries of provinces can be attributed in part to the fact that these authors were treating different groups of animals, but more important, the disagreement of boundaries reflects differences in the interpretation and application of the concept of biotic provinces.

The third method of faunal analysis is the ecological concept of the biome (Clements and Shelford, 1939). This concept has been thoroughly reviewed by Kendeigh (1961), according to whom a biome is "a biotic community characterized by distinctiveness in life-forms of the important climax species." Terrestrial biomes include such categories as coniferous forest, grassland, desert, and tropical forest, among others. These are, of course, discontinuous in their distribution on the surface of the earth. The "key" to the definition of the biome is the "life-form" of the vegetation. Thus, the biome is an ecological classification of major vegetational formations. Kendeigh (1961) refined the concept of biomes and distinguished various subdivisions, one of which, the biociation is defined as "a subdivision of a biome distinguished by uniformity and distinctiveness in the species composition of the climax community, particularly the animal predominants." This definition resembles that of the biotic province and is equally difficult to apply.

In the over-all scheme of geographic distribution, major assemblages of animals representing large faunal units show some agreement with the distribution of biociations; for example, the distributional limits of North American Herpetofaunas (Savage 1960) coincide at least in part, with the distribution of North American biociations as mapped by Kendeigh (1961:278).

When describing the distribution of a fauna in a given region, three salient features need to be taken into consideration.—1.) The distribution of the animal. 2.) The distribution of the animal's habitat. 3.) The distribution of the animal within its habitat. If the distributions of all animals in a given

habitat were the same as the limits of the habitat, then the concept of biotic provinces (biociations) would be perfectly applicable. But, such instances are rare. The distribution of a species of animal often is determined by factors other than the distribution of the animal's habitat. Means and rates of dispersal, presence of allopatric competitors, and presence of physical barriers, as well as various historical events may account for discrepancies in distributions. Objections to the use of each of the major methods of faunal analysis, each of which is based primarily on ecological premises, have been noted above. Actually, geographical analysis of faunas should be based primarily on physiographic data and secondarily on ecological premises.

Zoogeographers have divided the earth into faunal realms, each of which is divided into faunal regions, and each of which, in turn, is divided into faunal provinces. The faunal provinces are circumscribed by the limits of distributions of most of the members of a fauna that inhabits a certain usually continuous physiographic region. Thus, in western México there are three major physiographic provinces—the coastal plain, the highlands of the western sierras, and the tableland of the Mexican Plateau. Each of these three physiographic provinces has a distinctive herpetofauna, respectively, the Neotropical, the Sierra Madrean, and the Desert and Plains herpetofauna (Savage, 1960). In analyzing the patterns of distribution on a local basis, such as in Michoacán and adjacent areas of southwestern México, a more refined division is desirable. Faunal area has been used as a subdivision of a faunal province. For the purposes of the following analysis a faunal area is defined as a part of a faunal province characterized by an assemblage of species that differs from assemblages found elsewhere in the same faunal province.

The faunal areas in Michoacán approximate the physiographic areas outlined in the preceding description of the geography (see page 632). Each faunal area has characteristic species and/or assemblages of species different from species and/or assemblages in the other faunal areas. These faunal areas are discussed in detail below, where the fauna of each is described and analyzed.

Each faunal area can be described, and the species known to occur in the area can be listed, but such descriptions and lists do not afford an analysis of the fauna. In analyzing the faunas of adjacent or separated areas zoogeographers are interested to know the degree of faunal resemblance between the areas being considered. Several methods of determining the degree of faunal or taxonomic relationship have been proposed. Burt (1958) and Simpson (1960) have evaluated the various methods; Smith (1960) and Long (1963) have made further suggestions. Formulas that take into consideration both geographic and taxonomic levels are useful for measuring faunal resemblances. A comparison of the faunas of Eurasia and North America at the species level would indicate only a negligible amount of resemblance, and a comparison of the faunas of two mountain ranges in southern México at the family level would show only negligible differences, if any. In choosing a formula for determining faunal resemblances it is desirable to take into consideration the size of the faunas of each area, as well as the number of taxa common to both. Simpson (1960) evaluated various formulas and presented some new ideas for showing faunal similarities between regions. His methods of analysis based both on the presence and absence of taxa and their ecological distribution and abundance will be of use in areas where such detailed information is available. Sufficient data on local abundance of taxa

in Michoacán are lacking for that kind of analysis. The ecological distribution of a species is important for understanding its local distribution; paleoecological data are useful to draw inferences as to how the species could have established its present pattern of distribution. Neither this information, nor that concerning the relative abundance of taxa are of primary importance in determining the present faunal resemblance of one area to another. Only the presence or absence of taxa are of great significance. For this purpose the rather simple formula of Pirlot (1956) seems perfectly applicable, for it takes into account the number of taxa in each fauna and the number of taxa common to both faunas. The results of a formula used to show faunal resemblances have been termed amount of similarity, degree of relationship, and faunistic relation factor, among others. Smith (1960) proposed the last term, which, although it has merit, includes the word relation that can be confused with relationships in a strict phylogenetic sense. I suggest the modification of Smith's term to Faunal Resemblance Factor, which still retains his abbreviation FRF. By slightly modifying Pirlot's formula to reduce the factors to percentages, one step in the calculation can be omitted. The formula then reads:

$$\frac{2C}{N_1 + N_2} = \text{FRF},$$

where C = the number of taxa in common to the two areas, N_1 = the number of taxa present in one area, N_2 = the number of taxa present in the second area, and FRF = the Faunal Resemblance Factor. In this formula an FRF of 0 means that no taxa are common to the two areas, and an FRF of 1 means that all taxa are common to the two areas.

In an effort to present analyses of faunal resemblance in a graphic or tabular manner readily comprehensible to the reader, I have presented information on which the FRF is based, as well as the FRF itself (Tables 9-11). In these tables the geographic areas that are being analyzed are listed vertically on the left and horizontally in the same order across the top. In their common squares on the resulting grids the total number of species known from that area is set in bold-faced type. To the right and above the totals the numbers of species in common to each combination of faunal areas are set in roman type. To the left and below the totals the Faunal Resemblance Factors for each of the combinations are set in italic type. Throughout the following analysis of geographic distribution I have dealt only with species.

Use of this method reveals degrees of resemblance or dissimilarity between faunal areas, faunal provinces, or more diverse categories, and also shows the relative amount of resemblance within categories, as compared to that occurring between them. For example, examination of Table 9 shows that the FRF for the species of amphibians and reptiles in the three faunal provinces in Michoacán is low, ranging from .17 to .32, whereas the FRF for faunal areas within the Neotropical Province (Table 10) is much higher, ranging from .55 to .86.

Distribution of the Herpetofauna

In the following account the distribution of marine turtles and the sea snake in Michoacán is not included, but species that have not been found in Michoacán, but whose occurrence there is probable have been included. This review of distributions is on a geographic, not a systematic, basis. Many

species of amphibians and reptiles have similar distributions in Michoacán and adjacent areas; consequently, species with like distributions are grouped. Distributions are grouped into three basic patterns that roughly correspond to parts of three of the eight North American herpetofaunas recognized by Savage (1960); these are the Neotropical Herpetofauna in the lowlands, the Sierra Madrean Herpetofauna in the mountains, and the Desert and Plains Herpetofauna on the Mexican Pleateau. Two of these herpetofaunas contain assemblages of species having different patterns of distribution. For this reason the various assemblages are discussed separately, as outlined below:

Neotropical Herpetofauna
- Widespread Pacific Lowland Assemblage
- Pacific Coast Assemblage
- Balsas-Tepalcatepec Basin Assemblage

Sierra Madrean Herpetofauna
- Widespread Montane Assemblage
- Sierra Madre Occidental Assemblage
- Cordillera Volcánica Assemblage
- Sierra de Coalcomán Assemblage
- Sierra Madre del Sur Assemblage

Desert and Plains Herpetofauna

The distributions of many species fit well into the general patterns outlined above; others do not. Our knowledge of several of the latter is incomplete, or the species seemingly range across faunal boundaries is an incomprehensible pattern. In southwestern México there is faunal interchange between the Mexican Plateau and the Pacific lowlands, including the Balsas-Tepalcatepec Basin. On the basis of their over-all distributions or interspecific relationships, most of the species the distributions of which include the Mexican Plateau and the Pacific lowlands in southwestern México can be assigned to either the Desert and Plains Herpetofauna or to the Neotropical Herpetofauna. This aspect of distribution is discussed in detail in the section dealing with the Desert and Plains Herpetofauna. Three species (*Rana pipiens, Kinosternon integrum,* and *Lampropeltis doliata*) are wide-ranging and occur in all of the physiographic areas in Michoacán. In the lists of species given below they are omitted, but they are included in the succeeding analysis of the fauna. *Typhlops braminus* apparently is an introduced species and has not been included in the following discussion.

The bases for accounts of distribution are preserved specimens listed in the systematic study of the amphibians and reptiles of the state (Duellman, 1961). Distributional data for species in other parts of southwestern México were taken from unreported specimens and from a variety of published works, notably Duellman (1958) for Colima, Davis and Dixon (1959 and 1961) for Guerrero, and Davis and Smith (1953 a-c) for Morelos, as well as Smith and Taylor (1945, 1948, and 1950).

Neotropical Herpetofauna

In México the Neotropical Herpetofauna is composed of those species living in the tropical lowlands and the distributions of which, or the distributions of their relatives, extend southward into Central and South America. In Michoacán and adjacent parts of southwestern México species comprising this herpetofauna are found principally at elevations below 1000 meters. Three

faunal assemblages have different patterns of distribution in southwestern México—one assemblage in all of the lowland regions, another only on the coastal lowlands and lower mountain slopes, and a third in the Balsas-Tepalcatepec Basin and to a greater or lesser extent on the coastal lowlands. Each assemblage is discussed separately.

Widespread Pacific Lowland Assemblage.—Included in this assemblage are 35 species that are more or less widely distributed on the Pacific lowlands of México, including the Balsas-Tepalcatepec Basin. Many of the species occur in other lowland regions as well. For example, the distributions of five of the species extend to South America, 12 extend northward into the Mexican state of Sonora, and 13 include the lowlands in eastern México. On the other hand, some of the species range no farther northward than Colima and some no farther southward than Oaxaca, but all are found both to the north and to the south of Michoacán. The species included in this assemblage are:

Bufo marinus
Eleutherodactylus rugulosus
Leptodactylus melanonotus
Diaglena reticulata
Phyllomedusa dacnicolor
Smilisca baudini
Hyla smithi
Geoemyda pulcherrima
Geoemyda rubida
Coleonyx elegans
Phyllodactylus lanei
Anolis nebulosus
Basiliscus vittatus
Iguana iguana
Ctenosaura pectinata
Phrynosoma asio
Sceloporus horridus
Sceloporus melanorhinus
Sceloporus pyrocephalus
Mabuya brachypoda
Ameiva undulata
Heloderma horridum
Leptotyphlops phenops
Boa constrictor
Loxocemus bicolor
Conophis vittatus
Drymarchon corais
Drymobius margaritiferus
Imantodes gemmistratus
Leptophis diplotropis
Masticophis striolatus
Salvadora mexicana
Trimorphodon biscutatus
Agkistrodon bilineatus
Crotalus basilicus

Pacific Coastal Assemblage.—Seventeen species occur on the coastal lowlands and adjacent foothills, but do not occur in the Balsas-Tepalcatepec Basin. Most of these species are widely distributed throughout the coastal lowlands; the distributions of seven of the species extend southward into South America, four extend northward into the Mexican state of Sonora, and nine include the lowlands in eastern México. The species included in this assemblage are:

Bufo marmoreus
Phrynohyas inflata
Dryadophis melanolomus
Geagras redimitus
Hyla microcephala
Gastrophryne usta
Pseudemys scripta
Crocodylus acutus
Urosaurus bicarinatus
Scincella assata
Clelia clelia
Geatractus tecpanensis
Leptodeira septentrionalis
Manolepis putnami
Oxybelis aeneus
Sibon nebulatus
Natrix valida

Two other species (*Rhinophrynus dorsalis* and *Coniophanes fissidens*) are widespread in the lowlands of northern Central America and México, but reach the northern limits of their distributions on the coast of Michoacán. Four species (*Phyllodactylus homolepidurus, Anolis schmidti, Eumeces colimensis,* and *Eumeces parvulus*) have restricted distributions on the Pacific lowlands from Nayarit to Michoacán, where they reach the known southern limits of their ranges.

Twenty-four species occur on the coastal lowlands of Guerrero and southward, but are unknown from Michoacán; these are:

Dermophis multiplicatus
Bufo gemmifer
Syrrhophus pipilans
Hyla staufferi
Bipes tridactylum
Hemidactylus frenatus
Phyllodactylus delcampi
Anolis gadowi
Anolis subocularis
Anolis taylori
Sceloporus stejnegeri
Cnemidophorus guttatus
Cnemidophorus sacki
Ficimia publia
Leptodeira annulata
Leptodeira nigrofasciata
Leptophis mexicanus
Masticophis mentovarius
Salvadora lemniscata
Stenorrhina freminvilli
Tantilla martindelcampoi
Xenodon rhabdocephalus
Micrurus nigrocinctus
Micrurus nuchalis

On the coastal lowlands of Colima and northward there are six species, the distributions of which approach Michoacán, but do not cross the Río Coahuayana; these are *Bufo mazatlanensis, Syrrhophus modestus, Hypopachus oxyrrhinus, Leptotyphlops humilis, Dipsas gaigeae,* and *Micrurus diastema.*

Balsas-Tepalcatepec Basin Assemblage.—The large, arid, lowland basin lying inland to the Sierra de Coalcomán and the Sierra Madre del Sur has a distinctive herpetofaunal assemblage, including 13 endemic species. Eight of these endemics are found only in the Tepalcatepec Valley (indicated by an asterisk in the following list):

Bufo perplexus
Hypopachus caprimimus
Bipes canaliculatus
Phyllodactylus duellmani °
Phyllodactylus paucituberculatus °
Enyaliosaurus clarki °
Sceloporus gadowae
Urosaurus gadowi °
Eumeces altamirani °
Cnemidophorus calidipes °
Leptotyphlops bressoni °
Leptotyphlops gadowi °
Pseudoficimia pulcherrima

Eleven species are widely distributed in the Balsas-Tepalcatepec Basin and extend through the Ahuijullo depression to the lowlands of Colima and thence northward; five of these species range northward into Sonora; the species in this group are:

Tomodactylus nitidus
Pternohyla fodiens
Coniophanes lateritius
Hypsiglena torquata
Leptodeira latifasciata
Leptodeira splendida
Pseudoficimia frontalis
Sonora michoacanensis
Trimorphodon latifascia
Micrurus distans
Micrurus laticollaris

Four species have distributions similar to those listed above, but also occur on the coast of Michoacán; these are *Cnemidophorus communis, Cnemidophorus lineatissimus, Leptodeira maculata,* and *Tantilla calamaria.*

Five species are widely distributed on the coastal lowlands from Guerrero southward and occur also in the Balsas-Tepalcatepec Basin; these are *Bufo coccifer, Leptodactylus labialis, Crotalus durissus, Sceloporus siniferus,* and *Cnemidophorus deppei.* The last two species also occur on the southeastern part of coastal Michoacán.

Four species are known from the upper Balsas Basin in Morelos and Guerrero, but are unknown in the lower basin in Michoacán; these are *Hypopachus alboventer, Sceloporus ochoterenai, Cnemidophorus sacki,* and *Leptotyphlops maximus.*

Sierra Madrean Herpetofauna

The mountains of southwestern México can be divided into four separate highland masses—the Sierra Madre Occidental that parallels the Pacific coast from Sonora to Jalisco, the Sierra de Coalcomán in southern Michoacán, the Sierra Madre del Sur in southern Guerrero and Oaxaca, and the Cordillera Volcánica that extends from Michoacán to Veracruz. For purposes of faunal analysis the Cordillera Volcánica is divided into three regions—the Sierra de los Tarascos in central Michoacán, the Sierra Temazcaltepec in eastern Michoacán and the western part of the state of México, and the Sierra Ajusco in southern México and northern Morelos. Inhabiting the mountains of southwestern México is a rather distinctive assemblage of species that I consider to be a part of the Sierra Madrean Herpetofauna. Generally these species are distributed at elevations of more than 1000 meters; many do not descend to that elevation.

Mountainous regions often are characterized by a high amount of endemism in their faunas. The mountains in southwestern México are no exception. Fifty-one of the 98 species of amphibians and reptiles found there are not known to occur in other highland regions in Mexico. A finer analysis reveals 19 endemic species in the Sierra Madre del Sur, 12 in the Cordillera Volcánica, three in the Sierra de Coalcomán, and one in the southern part of the Sierra Madre Occidental.

Widespread Montane Assemblage.—Because of the many discontinuities in distributions, the description of distributional patterns in the highlands is more difficult than for the lowland fauna. The distribution of each of the 98 species known from the mountains of southwestern México is shown in Table 8. Of these, only six species occur in all of the highland regions—*Bufo occidentalis, Eleutherodactylus augusti, Hyla arenicolor, Hyla bistincta, Rana pipiens,* and *Rana pustulosa.*

Twenty-one species are widespread in the mountainous regions but are absent from one or both of the isolated mountain ranges, Sierra de Coalcomán and Sierra Madre del Sur. In the following list a single asterisk denotes species occurring in the Sierra de Coalcomán and two asterisks denote species occurring in the Sierra Madre del Sur; species not so marked are absent from both of the aforementioned mountain ranges, but occur widely through the Sierra Madre Occidental and the Cordillera Volcánica.

Pseudoeurycea belli °°
Microbatrachylus hobartsmithi
Phrynosoma orbiculaire
Sceloporus aeneus
Sceloporus grammicus °°
Sceloporus heterolepis °
Gerrhonotus imbricatus °
Conopsis biserialis
Rhadinaea laureata
Rhadinaea taeniata
Tantilla bocourti °°
Storeria storerioides °
Sceloporus scalaris
Sceloporus torquatus
Eumeces brevirostris
Eumeces dugesi
Eumeces indubitus
Thamnophis dorsalis °
Crotalus intermedius °°
Crotalus molossus
Crotalus triseriatus

Sierra Madre Occidental Assemblage.—The Sierra Madre Occidental extends roughly along a north-south axis for a distance of more than 1300 kilometers. The distributions of many species, such as *Bufo occidentalis, Eleutherodactylus augusti, Hyla arenicolor, Gerrhonotus imbricatus, Storeria storerioides, Thamnophis dorsalis,* and *Crotalus molossus,* include nearly the entire mountain mass. Other species, such as *Hyla bistincta, Sceloporus heterolepis,* and

TABLE 8.—DISTRIBUTION OF AMPHIBIANS AND REPTILES IN THE MOUNTAINS OF SOUTHWESTERN MÉXICO.

SPECIES	Sierra Madre Occidental	Cordillera Volcánica: Sierra de los Tarascos	Cordillera Volcánica: Sierra Temazcaltepec	Cordillera Volcánica: Sierra Ajusco	Sierra de Coalcomán	Sierra Madre del Sur
Ambystoma amblycephalum	—	X	—	—	—	—
Ambystoma ordinarium	X	X	X	—	—	—
Rhyacosiredon altamirani	—	—	—	X	—	—
Rhyacosiredon rivularis	—	—	—	X	—	—
Rhyacosiredon zempoalensis	—	—	—	X	—	—
Chiropterotriton chiropterus	—	—	—	X	—	—
Pseudoeurycea altamontana	—	—	—	X	—	—
Pseudoeurycea belli	X	X	X	X	—	X
Pseudoeurycea cephalica	—	—	—	X	—	—
Pseudoeurycea leprosa	—	—	—	X	—	—
Pseudoeurycea robertsi	—	—	X	—	—	—
Bufo occidentalis	X	X	X	X	X	X
Elcutherodactylus augusti	X	X	X	X	X	X
Eleutherodactylus calcitrans	—	—	—	—	—	X
Eleutherodactylus saltator	—	—	—	—	—	X
Microbatrachylus hobartsmithi	X	X	X	—	—	—
Microbatrachylus pygmaeus	—	—	—	—	X	X
Tomodactylus albolabris	—	—	—	—	—	X
Tomodactylus angustidigitorum	—	X	—	—	—	—
Tomodactylus dilatus	—	—	—	—	—	X
Tomodactylus fuscus	—	—	X	—	—	—
Tomodactylus grandis	—	—	—	X	—	—
Tomodactylus rufescens	—	—	—	—	X	—
Hyla arboricola	—	—	—	—	—	X
Hyla arenicolor	X	X	X	X	X	X
Hyla bistincta	X	X	X	X	X	X
Hyla erythromma	—	—	—	—	—	X
Hyla lafrentzi	—	X	X	X	—	—
Hyla mclanomma	—	—	—	—	—	X
Hyla smaragdina	—	X	—	—	X	—
Ptychohyla leonhardschultzei	—	—	—	—	—	X
Cochranella viridissima	—	—	—	—	—	X
Rana pipiens	X	X	X	X	X	X
Rana pustulosa	X	X	—	—	X	X
Rana sierramadrensis	—	—	—	—	—	X
Kinosternon integrum	—	X	—	—	X	X
Anolis dunni	—	—	—	—	X	X
Anolis liogaster	—	—	—	—	—	X
Anolis microlepidotus	—	—	—	—	—	X
Anolis omiltemanus	—	—	—	—	—	X
Phrynosoma orbiculaire	X	—	—	X	—	—
Phrynosoma taurus	—	—	—	—	—	X
Sceloporus aeneus	X	X	X	X	—	—
Sceloporus asper	—	X	—	—	X	—
Sceloporus bulleri	X	—	—	—	X	—
Sceloporus formosus	—	—	—	—	—	X
Sceloporus grammicus	X	X	X	X	—	X
Sceloporus heterolepis	X	X	—	—	X	—
Sceloporus mucronatus	—	—	—	—	—	X

TABLE 8.—DISTRIBUTION OF AMPHIBIANS AND REPTILES IN THE MOUNTAINS OF SOUTHWESTERN MÉXICO.—*Concluded*

SPECIES	Sierra Madre Occidental	Cordillera Volcánica: Sierra de los Tarascos	Cordillera Volcánica: Sierra Tenazcaltepec	Cordillera Volcánica: Sierra Ajusco	Sierra de Coalcomán	Sierra Madre del Sur
Sceloporus scalaris	X	X	X	X	—	—
Sceloporus torquatus	X	X	X	X	—	—
Sceloporus yarrowi	—	—	—	X	—	—
Eumeces brevirostris	X	—	—	X	—	—
Eumeces copei	—	X	X	X	—	—
Eumeces dugesi	X	X	X	—	—	—
Eumeces indubitus	X	—	X	—	—	—
Eumeces ochoterenai	—	—	—	—	—	X
Abronia deppei	—	—	—	—	—	X
Gerrhonotus gadowi	—	—	—	—	—	X
Gerrhonotus imbricatus	X	X	X	X	X	—
Gerrhonotus liocephalus	—	—	—	—	—	X
Chersodromus annulatus	—	—	—	—	—	X
Conopsis biserialis	X	X	X	X	—	—
Conopsis nasus	—	X	X	—	—	—
Enulius unicolor	—	X	X	X	X	—
Geophis bicolor	X	—	—	—	—	—
Geophis incomptus	—	—	—	—	X	—
Geophis maculiferus	—	X	—	—	—	—
Geophis nigrocinctus	—	—	—	—	X	—
Geophis omiltemanus	—	—	—	—	—	X
Geophis petersi	—	X	—	—	X	—
Geophis tarascae	—	X	—	—	—	—
Lampropeltis doliata	—	X	—	—	X	X
Pituophis lineaticollis	—	X	X	X	X	X
Rhadinaea aemula	—	—	—	—	—	X
Rhadinaea laureata	X	X	X	X	—	—
Rhadinaea omiltemana	—	—	—	—	—	X
Rhadinaea taeniata	X	X	—	—	—	—
Tantilla bocourti	X	X	X	X	—	X
Tantilla coronadoi	—	—	—	—	—	X
Tantilla deppei	—	—	—	X	—	X
Toluca conica	—	—	—	—	—	X
Toluca lineata	—	X	X	X	—	—
Tropidodipsas guerreroensis	—	—	—	—	—	X
Tropidodipsas occidentalis	—	—	—	—	X	—
Storeria storerioides	X	X	X	X	X	—
Thamnophis chrysocephalus	—	—	—	—	—	X
Thamnophis dorsalis	X	X	X	X	X	—
Thamnophis scalaris	—	X	X	X	—	—
Micrurus browni	—	—	—	—	—	X
Bothrops barbouri	—	—	—	—	—	X
Bothrops undulatus	—	—	—	—	—	X
Crotalus intermedius	X	X	—	—	—	X
Crotalus molossus	X	X	—	—	—	—
Crotalus pusillus	—	X	—	—	X	—
Crotalus transversus	—	—	—	X	—	—
Crotalus triseriatus	X	X	X	X	—	—
Sistrurus ravus	—	—	—	X	—	—

Rhadinaea taeniata, apparently are more restricted geographically. In analyzing the distributions of the amphibians and reptiles of the Sierra Madre Occidental, only the 31 species occurring, in the southern part of the sierra, Colima and Jalisco, are taken into account. *Geophis bicolor* apparently is endemic.

Cordillera Volcánica Assemblage.—The Cordillera Volcánica extends along a west-east axis for a distance of about 700 kilometers from Jalisco to Veracruz. The herpetofaunal assemblages of three ranges comprising the western part of the Cordillera Volcánica (Sierra de los Tarascos, Sierra de Temazcaltepec, and Sierra Ajusco) have been analyzed separately. The combined faunas of the three sierras consist of 59 species, of which 23 occur in all three ranges:

Pseudoeurycea belli
Bufo occidentalis
Eleutherodactylus augusti
Hyla arenicolor
Hyla bistincta
Hyla lafrentzi
Rana pipiens
Sceloporus aeneus
Sceloporus grammicus
Sceloporus scalaris
Sceloporus torquatus
Eumeces copei
Gerrhonotus imbricatus
Conopsis biserialis
Enulius unicolor
Pituophis lineaticollis
Rhadinaea laureata
Tantilla bocourti
Toluca lineata
Storeria storerioides
Thamnophis dorsalis
Thamnophis scalaris
Crotalus triseriatus

Forty-three species are found in the Sierra de los Tarascos; of these, *Ambystoma amblycephalum, Tomodactylus angustidigitorum, Geophis maculiferus,* and *Geophis tarascae* are endemic. Thirty-one species are known from the Sierra de Temazcaltepec; of these, *Pseudoeurycea robertsi* and *Tomodactylus fuscus* are endemic. Thirty-eight species are found in the Sierra Ajusco. Several of these, such as *Chiropterotriton chiropterus* and *Pseudoeurycea cephalica,* occur to the east in the Sierra Madre Oriental, but six species (*Rhyacosiredon altamirani, R. rivularis, R. zempoalensis, Pseudoeurycea altamontana, P. leprosa,* and *Tomodactylus grandis*) are endemic.

Sierra de Coalcomán Assemblage.—The isolated Sierra de Coalcomán extends roughly from west to east in southern Michoacán. Although these mountains probably are the least known faunistically of the highlands in southwestern México, 26 species of amphibians and reptiles have been found there. In addition to the six species that occur throughout the highlands of southwestern México, the Sierra de Coalcomán has six species in common with the Sierra Madre Occidental, 12 with the Cordillera Volcánica, and 11 with the Sierra Madre del Sur. *Tomodactylus rufescens, Geophis incomptus,* and *G. nigrocinctus* are endemic to the Sierra de Coalcomán.

Sierra Madre del Sur Assemblage.—The Sierra Madre del Sur lies along a west-northwest—east-southeast axis for a distance of about 700 kilometers from western Guerrero to southern Oaxaca. Although much of this highland is poorly known faunistically, the area in south-central Guerrero has been studied intensively. The fauna of that region forms the basis of comparison with faunas of the other highlands in southwestern México. Of the 45 species of amphibians and reptiles known from the central Guerrero part of the Sierra Madre del Sur, several species, such as *Cochranella viridissima, Sceloporus formosus,* and *Abronia deppei,* are northwestern representatives of groups that are more widespread to the southeast in México and Central America. The amount of endemism is high in the Sierra Madre del Sur; the following 19 species are known only from that range:

Eleutherodactylus calcitrans
Eleutherodactylus saltator
Tomodactylus albolabris
Tomodactylus dilatus
Hyla arboricola
Hyla melanomma
Rana sierramadrensis
Anolis liogaster
Anolis microlepidotus
Anolis omiltemanus
Phrynosoma taurus
Chersodromus annulatus
Geophis omiltemanus
Rhadinaea aemula
Rhadinaea omiltemana
Tantilla coronadoi
Tropidodipsas guerreroensis
Micrurus browni
Bothrops barbouri

Desert and Plains Herpetofauna

The central table-land or Mexican Plateau grades into the Chihuahuan Desert at elevations of about 1200 meters. Southward the plateau gradually rises to elevations of about 1900 meters in Michoacán and México. The western part of the Mexican Plateau is bordered on the south by the high mountains of the Cordillera Volcánica, but in the east the plateau continues past such formidable peaks as Popocatépetl and Ixtaccíhuatl and forms a broad plain at elevations from 1800 to 2000 meters in southern Puebla. The continuous high ridges of the Sierra Madre Oriental effectively eliminate faunal interchange between the Atlantic lowlands and the Mexican Plateau. In western México the mountains are not continuous; low passes and gradual slopes from the plateau to the lowlands allow faunal interchange between the lowlands of the Pacific coast and the Balsas Basin with the Mexican Plateau. The most conspicuous areas of faunal interchange are:

1. Western Jalisco, where the Sierra Madre Occidental is represented only by isolated volcanoes rising from the western edge of the plateau, which gradually diminishes in elevation to the coastal lowlands.
2. Upper Tepalcatepec Valley, where streams drain from the edge of the plateau south of Lago de Chapala into the lowland interior basin.
3. Tuxpan Valley in eastern Michoacán, where the Río Tuxpan drains southward into the Balsas Basin.
4. Upper Balsas Basin, where the lowland basin gradually merges with the plateau in southern Puebla.

Of the 45 species of amphibians and reptiles known to occur on the Mexican Plateau in Michoacán, 18 (40 per cent) are wide-ranging members of the Desert and Plains Herpetofauna; these species are:

Ambystoma tigrinum
Scaphiopus hammondi
Bufo compactilis
Hyla eximia
Rana pipiens
Kinosternon hirtipes
Sceloporus dugesi
Sceloporus spinosus
Cnemidophorus scalaris
Hypsiglena torquata
Lampropeltis doliata
Masticophis taeniatus
Pituophis deppei
Salvadora bairdi
Trimorphodon tau
Thamnophis dorsalis
Thamnophis eques
Thamnophis melanogaster

The ranges of twelve of the above species extend northward into the United States, and the ranges of three (*Ambystoma tigrinum, Rana pipiens,* and *Lampropeltis doliata*) extend to northeastern United States. Six of the species listed above (*Bufo compactilis, Cnemidophorus scalaris, Hypsiglena torquata, Masticophis taeniatus, Thamnophis eques,* and *Thamnophis melanogaster*) reach the southern limits of their distributions on the plateau in Michoacán.

Seven species (16 per cent of the fauna) are members of the Desert and

Plains Herpetofauna, but are endemic to the southern part of the plateau; these are:

Ambystoma dumerili
Tomodactylus angustidigitorum
Rana dunni
Rana megapoda
Rana montezumae
Geophis dugesi
Lampropeltis ruthveni

Ambystoma dumerili and the three species of *Rana* are restricted to lakes on the southern part of the plateau. *Rana montezumae* is the most widespread of these species, but in Lago de Pátzcuaro it apparently is replaced by *Rana dunni*. In Lago de Chapala *R. montezumae* and *R. megapoda* exist together to the apparent exclusion of *R. dunni*.

Pituophis lineaticollis and *Crotalus polystictus*, comprising four per cent of species on the plateau, range southward in the mountains and on the plateau; they reach the northern limits of their distributions in Michoacán.

Twelve (27 per cent) of the species occurring on the plateau are properly members of the lowland fauna, but these species have invaded the plateau, where in some places they are a conspicuous part of the herpetofauna. They are:

Leptodactylus occidentalis
Tomodactylus nitidus
Hyla smaragdina
Hypopachus caprimimus
Hypopachus oxyrrhinus
Kinosternon integrum
Anolis nebulosus
Urosaurus bicarinatus
Cnemidophorus costatus
Drymarchon corais
Elaphe triaspis
Masticophis striolatus

On the basis of their over-all distributions it is possible to ascertain where all but one of these species gain access to the plateau. *Leptodactylus occidentalis* and *Hypopachus oxyrrhinus* reach the southern limits of their distributions on the plateau in Michoacán; otherwise, they are found to the north at lower elevations. Apparently they reached the plateau via the Jalisco route. *Hyla smaragdina, Drymarchon corais, Elaphe triaspis,* and *Masticophis striolatus* are found on the southern part of the plateau in the area south of Lago de Chapala; evidently these species reached the plateau *via* the Tepalcatepec route. *Hypopachus caprimimus* occurs on the plateau only in the Tuxpan Valley, which it doubtless reached by way of the Río Tuxpan from the Balsas Basin, where the species is widespread. *Tomodactylus nitidus, Anolis nebulosus,* and *Urosaurus bicarinatus* occur on the plateau in the Chapala area and in the Tuxpan Valley, which they probably reach *via* the Tepalcatepec and Tuxpan routes, respectively. *Cnemidophorus costatus* apparently evolved in the Balsas Basin, from whence it dispersed *via* the Tepalcatepec route onto the plateau and thence northward to lower elevations via the Jalisco route. *Kinosternon integrum* is found in many areas on the plateau and could have gained access to the plateau by any one, or all, of the routes.

Six species (13 per cent) occurring on the plateau are more or less widely distributed in mountains bordering, or rising from, the plateau. Apparently, due to their wide ranges of tolerance, these species are able to descend onto the plateau:

Bufo occidentalis
Eleutherodactylus occidentalis
Hyla arenicolor
Sceloporus scalaris
Sceloporus torquatus
Crotalus triseriatus

Patterns of Distribution

Correlation of the general patterns of distribution of the herpetofauna with the principal animal habitats and physiographic regions is instructive. According to Savage's (1960) classification of North American herpetofaunas, which is provisionally used here, the amphibians and reptiles of Michoacán can be grouped into three of the prescribed faunas. The species inhabiting the lowlands are members of the Neotropical Herpetofauna; those inhabiting the mountains are members of the Sierra Madrean Herpetofauna, and those living on the Mexican Plateau are a part of the Desert and Plains Herpetofauna. Examination of Table 9 shows that although there is some continuity of distribution between these faunas, the faunas are distinct. Only 14 of the 101 species occurring on the lowlands in Michoacán occur also on the Mexican Plateau or in the mountains. As mentioned previously, some species, such as *Rana pipiens* and *Lampropeltis doliata,* because of their apparent wide range of tolerance to ecological factors, are widespread ecologically and geographically. Such species are difficult or impossible to place in any one fauna. The insignificant amount of specific similarity between the Neotropical Herpetofauna and the Sierra Madrean and Desert and Plains herpetofaunas strongly suggests that the distributional patterns of the species comprising the Neotropical Herpetofauna are unrelated to those in the other faunas.

TABLE 9.—MEASURE OF FAUNAL RESEMBLANCE OF THREE MAJOR HERPETOFAUNAS IN MICHOACÁN.

Species in Common / Faunal Resemblance Factor	Lowlands *Neotropical Fauna*	Mexican Plateau *Desert and Plains Fauna*	Mountains *Sierra Madrean Fauna*
Lowlands *Neotropical Fauna*	**101**	14	14
Mexican Plateau *Desert and Plains Fauna*	*0.19*	**45**	18
Mountains *Sierra Madrean Fauna*	*0.17*	*0.32*	**68**

It has been demonstrated that the Neotropical Herpetofauna living in the lowlands of southwestern México is independent of the faunas in the mountains and on the Mexican Plateau. The primary division of the lowlands is into the coastal lowlands and the interior Balsas-Tepalcatepec Basin. The coastal lowlands are divided into three regions—the coastal lowlands of Guerrero southeastward, the coastal lowlands of Michoacán, and the coastal lowlands of

Colima northward. The Balsas-Tepalcatepec Basin is divided into two regions —the Tepalcatepec Valley and the Upper Balsas Basin, making five regions in all. There is considerable continuity of distribution throughout the lowlands, for the Faunal Resemblance Factors (FRF) range from 0.55 to 0.86 and average 0.69 (Table 10).

On the coastal lowlands of southwestern México in the states of Colima, Michoacán, and Guerrero, 113 species of amphibians and reptiles are known, and 57 of them (50.4 per cent) reach the limits of their distributions there. Twenty-eight species that occur on the coastal lowlands of Guerrero and southeastward apparently do not cross the Río Balsas into Michoacán, and eight species known from the coastal lowlands of Michoacán and northward apparently do not cross the Río Balsas into Guerrero. Four species that occur on the coastal lowlands of Michoacán and Guerrero evidently do not cross the Río Coahuayana into Colima, whereas 17 species that occur on the coastal lowlands of Colima and northward apparently do not cross the Río Coahuayana into Michoacán. The FRF between coastal Guerrero and Michoacán is 0.77, whereas the FRF for Michoacán as compared with Colima is 0.85 (Table 10). These data indicate that the Río Balsas is an important barrier to dispersal on the coastal lowlands and that the Río Coahuayana is not so effective a barrier as is the Río Balsas. Limits of distribution are reached by 36 species at the Río Balsas and by 21 species at the Río Coahuayana, even though there are no apparent ecological changes at these places.

Table 10.—Measure of Faunal Resemblance of Herpetofaunas of the Lowlands in Southwestern México.

Species in Common / Faunal Resemblance Factor	Coastal Guerrero southward	Coastal Michoacán	Coastal Colima northward	Tepalcatepec Valley	Upper Balsas Basin
Coastal Guerrero southward...	**88**	60	56	44	42
Coastal Michoacán.....	*0.77*	**68**	64	45	41
Coastal Colima northward.....	*0.65*	*0.85*	**83**	54	50
Tepalcatepec Valley.....	*0.55*	*0.64*	*0.70*	**72**	58
Upper Balsas Basin.....	*0.56*	*0.63*	*0.69*	*0.86*	**62**

Seventy-six species inhabit the Balsas-Tepalcatepec Basin; 58 (76 per cent) of these occur in both the Tepalcatepec Valley and in the Upper Balsas Basin. Four species are endemic to the Upper Balsas Basin; eight are endemic to the Tepalcatepec Valley, and five others are restricted to the basin. The presence of 54 species on the coastal lowlands that do not occur in the basin, plus the presence of 17 endemic species in the basin, show that there is a significant

faunal discontinuity between the coastal lowlands and the interior basin; the FRF is 0.62. When the fauna of the Balsas-Tepalcatepec Basin is compared with the faunas of the various coastal regions in southwestern México, it is evident that the greatest resemblance is with the fauna of the lowlands of Colima northward, and not with the geographically closer lowlands of Michoacán and Guerrero (Table 10). This resemblance apparently is due to past, as well as present, faunal interchange via the Ahuijullo depression at the western end of the Tepalcatepec Valley. Evidently this lowland connection between the interior basin and the coastal lowlands has been a more important dispersal route than the probably more recent lower Balsas gorge. The animal habitats in the Balsas-Tepalcatepec Basin resemble those on the coastal lowlands, but are more arid, and Tropical Semi-deciduous Forest is limited to gallery forests along the major rivers. These ecological differences probably account for some of the faunal differences between the basin and the coastal lowlands, but the absence of many species in habitats in the basin that the species occupy on the coastal lowlands suggests that the partial geographic isolation of the basin is the primary cause for the faunal differences.

An analysis of the highland faunas in southwestern México shows a gradual faunal replacement (Tables 8 and 11) from west to east from the Sierra Madre Occidental to the Sierra Ajusco *via* the Sierra de los Tarascos and Sierra de Temazcaltepec. Of the highlands rising from, or bordering, the Mexican Plateau in southwestern México, the Sierra Ajusco has the most distinctive fauna, for included in it are several species of salamanders either ranging eastward or related to species occurring to the east in the Sierra Madre Oriental. The continuity of montane environments through the Cordillera Volcánica is shown by the high degree of faunal resemblance between the various mountain ranges (FRF, 0.68 between the Sierra Ajusco and the Sierra de Temazcaltepec, 0.74 between the Sierra de Temazcaltepec and the Sierra de los Tarascos, and 0.70 between the Sierra de los Tarascos and the Sierra Madre Occidental). On the basis of present continuity of environments and similar geological histories of the ranges in the Cordillera Volcánica and the Sierra Madre Occidental, the close resemblance of highland faunas in the adjacent ranges was expected (variation in FRF is 0.55 to 0.74; average, 0.66).

The Sierra de Coalcomán and the Sierra Madre del Sur are presently isolated from one another and from the Cordillera Volcánica and the Sierra Madre Occidental, although the Sierra Madre del Sur has a highland connection with the Sierra Madre Oriental in Oaxaca. The variation in FRF is 0.24 to 0.42 (average, 0.30) between the isolated ranges and all other highlands analyzed in southwestern México. Of the 26 species known to occur in the Sierra de Coalcomán, 12 occur also in the Sierra Madre Occidental (FRF, 0.42), and 18 species occur in the Cordillera Volcánica (FRF, 0.42), although a comparison of the fauna of the Sierra de Coalcomán with any one of the ranges in the Cordillera Volcánica results in a lower FRF (0.31 to 0.36). Eleven species are common to the highland faunas of the Sierra de Coalcomán and the Sierra Madre del Sur (FRF, 0.31), whereas there is less resemblance between the Sierra Madre del Sur and the other highlands analyzed (Table 11). Altitude is an important factor when comparing the fauna of southern Michoacán with that of southern Guerrero; for example, the FRF between the lowland faunas is 0.77, that between the faunas of moderate elevations is 0.48, and that between the faunas of the higest

Table 11.—Measure of Faunal Resemblance of Herpetofaunas of the Mountains in Southwestern México.

Species in Common / Faunal Resemblance Factor	Sierra Madre Occidental	Sierra de los Tarascos	Sierra de Temazcaltepec	Sierra Ajusco	Sierra de Coalcomán	Sierra Madre del Sur
Sierra Madre Occidental	**31**	26	21	19	12	10
Sierra de los Tarascos	*0.70*	**43**	27	23	11	11
Sierra de Temazcaltepec	*0.69*	*0.74*	**30**	23	10	9
Sierra Ajusco	*0.55*	*0.57*	*0.68*	**38**	10	10
Sierra de Coalcomán	*0.42*	*0.32*	*0.36*	*0.31*	**26**	11
Sierra Madre del Sur	*0.26*	*0.25*	*0.24*	*0.24*	*0.31*	**45**

elevations is 0.22 (Table 12). The distribution of habitats is insignificant in analyzing the distribution of the herpetofauna in the highlands. In each of the highlands studied fir forest exists on the highest peaks, yet typical inhabitants of the fir forest in the Cordillera Volcánica, such as *Pseudoeurycea belli, Hyla lafrentzi,* and *Sceloporus aeneus,* are absent from the Sierra de Coalcomán. Distinct species occupy corresponding ecological niches in different mountain ranges; for example, *Sceloporus torquatus* in the Cordillera Volcánica is replaced by *S. bulleri* in the Sierra de Coalcomán and by *S. mucronatus* in the Sierra Madre del Sur. The niches in some mountain ranges apparently are not filled; for example, not one of the three species of *Eumeces* living in the pine forests in the Cordillera Volcánica has been found in the Sierra de Coalcomán. The physiographic isolation of the various mountain ranges, especially the Sierra de Coalcomán and the Sierra Madre del Sur, is the primary reason for the observed faunal resemblances.

The herpetofauna of the Mexican Plateau in Michoacán is a mixture of species that are widespread on the plateau and species that are endemic to the southern part of the plateau, plus some invaders both from the highlands and lowlands. All of the invaders apparently are species of wide ecological tolerances, whereas those species that inhabit only the plateau are, at least in Michoacán, usually more restricted in their ecological distribution. The endemism on the southern part of the plateau can be accounted for by the presence of large lakes, which in the past were more extensive than they are now. Four of the seven endemics are aquatic.

Although ecological factors are of some importance in the broad patterns of distribution of amphibians and reptiles in southwestern México, the basic patterns are more closely correlated with the physiography. In order to understand this correlation a person needs to interpret the present distributions

TABLE 12.—AMOUNT OF FAUNAL RESEMBLANCE BETWEEN FAUNAS AT DIFFERENT ELEVATONS IN THE SIERRA DE COALCOMÁN AND THE SIERRA MADRE DEL SUR.

ELEVATION	Sierra de Coalcomán (No. species)	Sierra Madre del Sur (No. species)	Species in common	Faunal Resemblance Factor
Lowlands 0–800 meters	68	88	60	0.77
Moderate 800–1500 meters	21	37	14	0.48
Highlands 1500–2300 meters	15	30	5	0.22

in light of the evolutionary histories of the faunas and past events in the development of the present land forms.

ORIGIN OF THE HERPETOFAUNA

The amphibians and reptiles inhabiting Michoacán belong to three herpetofaunal units—Neotropical, Sierra Madrean, and Desert and Plains—as defined by Savage (1960). An analysis of these faunal elements has shown that they are generally distinctive in Michoacán and that each can be subdivided into geographic units. Further analysis of the fauna can result in a determination of the establishment of the present patterns of distribution, but before such an analysis can be completed, an effort must be made to determine the origin of the faunal components.

The lack of a fossil record of Mexican amphibians and reptiles, and inadequate knowledge of the historical geology of the country, greatly limits the extent and solidarity of any conclusion. In attempting to explain the origin of the herpetofauna, it is necessary to utilize the few historical facts, to extrapolate from what is known of the fossil record of better known groups of animals (for example, the mammals), and to use what is available on the distributions and supposed phylogenetic relationships of the extant species.

Since the publication of Dunn's (1931) geographic arrangement of the American herpetofauna, it has been customary for faunistic writers to analyze the components of their faunas according to his scheme. Since 1931 Dunn's arrangement has been broadened, criticized, and modified by a number of workers, principally Schmidt (1943), Simpson (1943), and Stuart (1932, 1950, and 1957). Other workers have misapplied Dunn's ideas. He suggested that the escarpment of the Mexican Plateau marked a line between the Nearctic and the Neotropical realms, but pointed out that members of many groups of North American origin had passed south of that line and penetrated well into South America, and that members of some South American groups had crossed the line and dispersed northwards. He analyzed the herpetological

fauna in order to see if it fitted the analysis of the mammalian fauna made by Matthew (1915). Dunn's arrangement was surprisingly similar to Matthew's but by no means so clear cut, and with many more doubtful cases.

Schmidt (1943) modified Dunn's arrangement by introducing the idea that lower North America was a paleopeninsula, into which older and weaker groups were crowded throughout the period of separation of North and South America and mentioned some "hanging relicts" still there that had not moved south when the continents were connected. Stuart (1950 and 1957) further modified Dunn's arrangement by introducing the concept of another faunal element—the Autochthonous Middle American Element. Stuart pointed out that many families of amphibians and reptiles were equally well represented in South America and Middle America, or in North America and Middle America. He suggested that Middle America was an important center of evolution for Schmidt's "hanging relicts."

One of the weakest aspects of Dunn's arrangement was his disposition of the colubrid snakes. The family has an immense number of genera and species and is in a chaotic state insofar as an understanding of the phylogenetic relationships of the genera and suprageneric categories is concerned. Stuart (1932 and 1950), in a sense, improved on Dunn's ideas on the colubrid snakes. Dunn's arrangement was at a family level, whereas Stuart's in large part was on an infra-familial, generic, and in some instances even on a species-group level. Both methods have their merit. A conservative arrangement of the families in the Middle American herpetofauna would retain *Claudius* and *Staurotypus* in the Kinosternidae and not place them in a separate family, the Staurotypidae, as has been done by some workers. By such an arrangement the elements that could possibly be called Autochthonous Middle American families are the following: 1) Rhinophrynidae, a monotypic family having *Rhinophrynus dorsalis* distributed from Tamaulipas and Michoacán, México, southward into Costa Rica; 2) Dermatemydidae, represented by only one

Table 13.—Historical Arrangement of the Families of Amphibians and Reptiles of Michoacán According to Dunn's (1931) Scheme. (An asterisk indicates that the family is both Old Northern and South American.)

Old Northern (of Dunn)	South American (of Dunn)
Ambystomatidae	Leptodactylidae
Plethodontidae	Hylidae
Rhinophrynidae	Microhylidae
Pelobatidae	Amphisbaenidae
Bufonidae	Gekkonidae
Ranidae	Iguanidae*
Kinosternidae	Teiidae
Emydidae	Typhlopidae
Crocodylidae	Leptotyphlopidae
Eublepharidae	Boidae
Iguanidae*	Colubridae*
Scincidae	Elapidae
Anguidae	
Helodermatidae	
Colubridae*	
Crotalidae	

living species, *Dermatemys mawi,* ranging from Veracruz to Honduras; 3) Anelytropsidae, a monotypic family having *Anelytropsis papillosus* known from a few localities in eastern México; 4) Xenosauridae, having four species of *Xenosaurus* distributed to eastern México and Guatemala; 5) Helodermatidae, having two species ranging from southwestern United States into Guatemala. Thus, only five of 50 New World families (and only nine species) are referable to Stuart's Middle American Element. Nevertheless, if the faunal elements are examined at the generic level, much is to be gained from Stuart's arrangement.

The families of amphibians and reptiles occurring in Michoacán are listed according to Dunn's arrangement in Table 13, whereas the genera are listed in accordance with Stuart's inclusion of the Autochthonous Middle American Element in Table 14. Examination of Table 13, which follows Dunn's arrangement, shows that the herpetofauna of Michoacán is about equally divided between South American and Old Northern families. Stuart's arrangement of genera, including the Autochthonous Middle America Element, (Table 14) reveals a noticeably smaller Middle American group, and a still smaller South Amercan group. Most of the North American genera are distributed primarily in México and northward; 31 percent of the genera reach the southern limits of their distributions in México, and 28 per cent of them extend into South America. Of the Middle American genera, 65 per cent extend into South America. The data from the genera of the herpetofauna of Michoacán support Hershkovitz's (1958:587) idea that southwestern México is a transition zone between the Neotropical and Nearctic mammalian faunas.

Savage (1960) defined five major historical elements of the North American herpetofauna and correlated them with the geofloras of North America. Unfortunately, from central México southward the herpetofaunas and their geofloral associates are highly speculative. If Savage's arrangement were followed, the genera listed as "North American" in Table 14 would be placed in three categories in two major faunal elements. The Old Northern Faunal Element is associated with the Arcto-Tertiary Geoflora and contains four herpetofaunal complexes, only one of which, the Central American Complex, is present in Michoacán. Included in this complex are genera such as *Pseudoeurycea, Conopsis, Pseudoficimia,* and *Toluca.* As inhabitants of the cool temperate Arcto-Tertiary Geoflora, these genera were differentiating at the time of the major tectonic changes in México in the Miocene and Pliocene. The Young Northern Element is associated with the Madro-Tertiary Geoflora and contains two groups—the Madrean Herpetofauna complex and the Desert and Plains Herpetofaunal Complex. According to Axelrod (1958) the Madro-Tertiary Geoflora originated in the Middle Eocene and radiated from the "Sierra Madre of México," from whence it reached its greatest expansion in the Pliocene. The Madrean Complex is associated with the subhumid montane environments and in Michoacán includes such groups as *Gerrhonotus, Sceloporus torquatus* group, and *Crotalus triseriatus* group. The Desert and Plains Complex is associated with arid and semiarid environments in the southwestern United States, the Mexican Plateau, and to a lesser extent the Pacific Coastal Plain of western México. In Michoacán genera such as *Scaphiopus, Phrynosoma, Urosaurus, Pituophis,* and *Salvadora* belong in this group. Other categories in Savage's arrangement correspond to those of Stuart. Thus, aside from the two faunal elements discussed above, Michoacán has representatives

Table 14.—Historical Arrangement of the Genera of Amphibians and Reptiles of Michoacán. (Genera enclosed in parentheses have been derived from stocks in the geographical category in which they are listed.)

North American	Middle American	South American
Ambystoma	*Rhinophrynus*	*Leptodactylus*
Pseudoeurycea	*Eleutherodactylus* (part)	*Eleutherodactylus* (part)
Scaphiopus	*Hyla* (part)	(*Microbatrachylus*)
Bufo	*Phyllomedusa* (part)	(*Tomodactylus*)
Hyla (part)	*Gastrophryne*	*Hyla* (part)
Pternohyla	*Hypopachus*	(*Diaglena*)
Rana	*Crocodylus*	*Phyllomedusa* (part)
Kinosternon	*Anolis* (part)	*Phrynohyas*
Geoemyda	*Basiliscus*	(*Bipes*)
Pseudemys	*Iguana*	*Phyllodactylus*
Coleonyx	*Ctenosaura*	*Anolis* (part)
Phrynosoma	*Enyaliosaurus*	*Ameiva*
Sceloporus	*Mabuya*	*Typhlops*
Urosaurus	*Scincella*	*Leptotyphlops*
Eumeces	*Cnemidophorus* (part)	*Boa*
Cnemidophorus (part)	*Loxocemus*	*Clelia*
Heloderma	*Coniophanes*	*Dryadophis*
Gerrhonotus	*Conophis*	*Drymarchon*
Conopsis	*Geophis*	*Drymobius*
Diadophis	*Imantodes*	
Elaphe	*Leptophis*	
Enulius	*Oxybelis*	
Geagras	*Rhadinaea*	
Geatractus	*Sibon*	
Hypsiglena	*Tantilla*	
Lampropeltis	*Micrurus*	
Leptodeira		
Manolepis		
Masticophis		
Pituophis		
Pseudoficimia		
Salvadora		
Sonora		
Toluca		
Trimorphodon		
Tropidodipsas		
Natrix		
Storeria		
Thamnophis		
Agkistrodon		
Crotalis		

of the Middle American Element and the South American Element. The Middle American Element was associated with the Neotropical Tertiary Geoflora; included in this element are genera such as *Rhinophrynus, Hypopachus, Basiliscus, Enyaliosaurus, Imantodes, Leptophis, Rhadinaea,* and *Tantilla.* According to Stuart (1950) the Autochthonous Middle American Herpetofauna developed in nuclear Central America at the same time related groups were differentiating in South America, which was separated from Central America by a sea portal from late Paleocene to mid-Pliocene. The South American Element also is associated with the Neotropical Tertiary Geoflora; included in this element are such inhabitants of Michoacán as

Leptodactylus, Phrynohyas, Ameiva, Typhlops, Boa, and *Dryadophis.* Most, if not all, members of the South American Element that are now present in Central America and México probably extended their ranges northward from South America after the Panamanian and Colombian portals closed in mid-Pliocene [see Simpson (1953) for a discussion of these portals]. Consequently, these genera probably only recently entered southwestern México, although they are members of the oldest faunal element.

Whether the herpetofauna is analyzed on the basis of Dunn's arrangement at the family level, Stuart's arrangement including three faunal elements in southern México and Central America, or Savage's association of four elements (excluding Holarctic) with geofloras, the same basic result is obtained: the herpetofauna of Michoacán contains members of both southern and northern faunal elements, the latter being predominant. The transitional nature of the herpetofauna coincides with the diversity of tropical and temperate environments and the geographic position of the state with regard to the tropical lowlands and the Mexican highlands.

The multiplicity of species of some genera, such as *Sceloporus, Thamnophis,* and *Crotalus,* on the southern part of the Mexican Plateau and adjacent mountain ranges has been the basis on which some authors, notably Smith (1939), Ruthven (1908), and Gloyd (1940) have suggested that the southern part of the Mexican Plateau was the center of origin of these genera. Schmidt (1943) suggested that the Mexican Plateau was a paleopeninsula into which many groups were crowded during the separation of North America from Central America and México. Subsequently, Pleistocene cooling also forced warmth-adapted groups southward. Perhaps many of these genera underwent considerable differentiation in southern México, but most of them probably originated farther north.

ORIGIN OF PRESENT PATTERNS OF DISTRIBUTION

Some of the interesting patterns of distribution include the following: 1) absence of salamanders, skinks of the genus *Eumeces,* and snakes of the genera *Conopsis* and *Toluca* in the Sierra de Coalcomán; 2) high degree of faunal affinity between the Balsas-Tepalcatepec Basin and the Pacific lowlands from Colima northward; and 3) different montane faunas in the Cordillera Volcánica, Sierra de Coalcomán, and Sierra Madre del Sur. These have been treated in the section on the distribution of the herpetofauna.

Pleistocene Biogeography

The geology of the Pleistocene is well known for some parts of the United States and Canada [see Flint (1957) for a thorough summary]; Pliocene and Pleistocene climates in North American have been reviewed by Dorf (1959) and Hibbard (1960). Palynological studies have been reported from various parts of southwestern United States by Clisby and Sears (1956), Potzger and Tharp (1947, 1954), and Hevly and Martin (1961). Martin, Schoenwetter, and Arms (1961) reviewed the palynology of postglacial deposits in the southwestern United States. The works cited above, together with many others, provide a wealth of data, sometimes contradictory, concerning Pleistocene and postglacial climates and ecology in southwestern United States, but the historical changes in climates and environments in southwestern

México can only be partially inferred from these works, for little information is available from southern México. Evidence from sedimentary studies in the Valley of México (Sears, Foreman, and Clisby, 1955) and at Lago de Pátzcuaro (Hutchinson, Patrick, and Deevey, 1956) suggests drastic climatic shifts in the montane regions of southern México in the Pleistocene. Additional evidence for climatic and ecological fluctuation was provided by Martin and Harrell (1957) and Martin (1958b), who postulated that vertical displacement of environments in southern México at the time of the Glacial Maximum could have been as much as 3,000 feet. White (1956) demonstrated the presence of Pleistocene montane glaciers on the volcanoes in southern México, and DeTerra, Romero, and Steward (1949) noted evidence for successive glacial advances on Ixtaccíhuatl. These authors correlated the Salto Advance with the Iowan Glacial. At that time ice extended down to about 3100 meters, approximately 1500 meters below the present snow line. Martin, Robins, and Heed (1954), Martin (1958a), Martin and Harrell (1957), and Duellman (1960b) discussed Pleistocene biogeography in relation to present vegetation zones and their animal associates. Although inconclusive, the evidence for large vertical shifts in environments in the mountainous regions of southern México seems to be valid, but Duellman (1960b) suggested that at lower elevations, especially in coastal areas, where the climate is moderated by onshore winds, vertical shifts in environments may have been much less.

Postglacial climates in the United States included a warm and dry period, the Thermal Maximum or Xerothermic, extending from about 9,500 to 2,000 years ago (Deevey and Flint, 1957), but Martin (1958b) concluded that there is no sound evidence for drought on the Mexican Plateau. In North America pluvial conditions are usually correlated with glacial times, but changes in the over-all pattern of high and low pressure areas at the time of extensive continental glaciation may have sufficiently altered the cyclonic winds in México and northern Central America to modify the pattern of cool-moist versus warm-dry climates.

Martin (1958b) suggested that some of the best evidence for climatic change in México and Central America is found in the relict distributional patterns of plants and animals. Supporting data of this kind have been given by Burt (1949) and Blair (1958) for mammals, Martin, Robins, and Heed (1954) for birds, and Martin (1958a) and Duellman (1960b) for amphibians and reptiles. Present patterns of distributions of amphibians and reptiles in Michoacán can be correlated, in part, with probable climatic changes in Pleistocene and postglacial times.

On the basis of the evidence for montane glaciers on Ixtaccíhuatl and Popocatépetl and the presence of fossil pollens of such cold-adapted trees as spruce (*Picea*) in the Valley of México in Wisconsin time (Sears, Foreman, and Clisby, 1955), it is safe to assume that climates on the southern part of the Mexican Plateau and in the bordering cordilleras were much cooler in the glacial stages than they are now. For example, spruce is primarily a boreal tree, which extends southward at high elevations in the Rocky Mountains to southern Arizona. In México spruce is not now known to occur south of the Sierra Madre Occidental in Chihuahua; subalpine conifers immediately below treeline in the Cordillera Volcánica now include *Pinus, Abies,* and *Cupressus* (Martin, 1958b).

Cool climates in glacial times and concomitant depression of vegetation zones by nearly 1000 meters would have drastically altered the distribution

of the major animal habitats in the highlands of southwestern México. In fact, a downward shift of about 500 meters would be sufficient to have coniferous forest covering the entire southern part of the Mexican Plateau and a fir forest continuous, or nearly so, in the Cordillera Volcánica. Also, a depression of environments of no more than 500 meters would have resulted in a continuous pine-oak forest across the Ahuijullo depression between the Cordillera Volcánica and the Sierra de Coalcomán.

On the basis of the historical evidence and the present patterns of distribution of amphibians and reptiles, I suggest that at the Glacial Maximum the distribution of animal habitats in Michoacán and adjacent areas was modified as follows:

1.—Permanent snow on the highest mountains, such as Cerro Tancítaro and Cerro San Andrés and an Arctic-alpine environment between the snow and the tree line.

2.—Nearly continuous fir forest, probably containing spruce, along the high ridges in the Sierra Madre Occidental and the Cordillera Volcánica; a large expanse of fir forest in the Sierra de Coalcomán separated from the fir forest in other ranges.

3.—Pine-oak forest at moderate elevations on the slopes of the Sierra de Coalcomán and the Cordillera Volcánica in areas where arid tropical scrub forest now exists; a continuity of pine-oak forest in the Ahuijullo depression between the Sierra de Coalcomán and the Cordillera Volcánica.

4.—Nearly continuous forest dominated by pine, but having locally a mixture of pine and fir or pine and oak, on the Mexican Plateau.

5.—Tropical semi-deciduous forests nearly continuous along the lower slopes of the Sierra de Coalcomán and coastal lowlands from at least Nayarit southward.

6.—Arid tropical scrub forest only in the lower parts of the Balsas-Tepalcatepec Basin and in isolated areas on the coastal lowlands.

At the height of glacial retreat, when climates were warmer, and in some areas probably drier, than they are now, I visualize the distribution of animal habits in Michoacán to have been altered, as follows:

1.—Fir forest only on the tops of the highest mountains, perhaps absent from the Sierra de Coalcomán.

2.—Pine-oak forest on the mountains at elevations of about 1300 meters or more, not continuous across the Ahuijullo depression.

3.—Pine-oak savanna on the southern part of the Mexican Plateau.

4.—Tropical semi-deciduous forest only in barrancas in the windward slopes of the Sierra de Coalcomán.

5.—Dense arid tropical scrub forest on the coastal lowlands and to elevations of about 1300 meters in the Balsas-Tepalcatepec Basin.

Although Martin (1958b) thought that there was no good evidence for drought on the Mexican Plateau at the time of the Thermal Maximum (9,500 to 2,000 years ago), I suggest that the xeric conditions prevalent there now are the result of gradually drier climatic conditions in postglacial times. Even within historic times, we know that many of the lakes have shriveled in size and others have filled with sediment. How much of the apparent aridity is caused by poor soils due to centuries of tilling and planting and more recently due to over-grazing is difficult to say, but judging solely on the basis of present distributions of aquatic and aquatic-margin animals (*Ambystoma*, *Rana*, and *Kinosternon*, as examples) more mesic conditions must have prevailed since the last glacial stage.

The development of the open arid tropical scrub forest under extremely xeric conditions in the Balsas-Tepalcatepec Basin also seems to be rather recent; probably this is a result solely of gradual climatic desiccation, for the physical features of the landscape that produce the strong rain shadow in the basin have been in existence since before the Pleistocene.

A complicating factor in southwestern México is the presence of many volcanoes. Carreño (1943) stated that Cerro Tancítaro, Nevado de Colima, Nevado de Toluca, and most of the other large cones in the Cordillera Volcánica were formed in the Pliocene. Volcán Jorullo was formed in 1759, and eruption ceased in 1775. Volcán Colima has erupted many times since Spanish colonization; the last eruption was in 1941. Volcán Parícutin was formed in 1943 and ceased activity in 1951. Probably volcanic activity has been in progress ever since the formation of the major cones in the Pliocene. Lava flows and deep deposits of ash obviously affect the vegetation and fauna [see Burt (1961) for a discussion of the biological effects of Volcán Parícutin].

Dispersal Routes in Southwestern México

It seems to me that none of the major geological changes in the past was significant in directly affecting dispersal routes, but certainly the environmental fluctuations in the Pleistocene markedly influenced animal dispersal in southwestern México. Animal dispersal routes in southwestern México probably are the result of the complex geography and Pleistocene and postglacial climatic changes.

When estimating dispersal routes into a given area, I considered the absence of certain species to be as important as the presence of other species.

Among the major lowland dispersal routes in southwestern México, the coastal lowland route is the most obvious. The large number of species that occur along the coast from north of Colima to Guerrero and southward attest to the general uniformity of environmental conditions and to the lack of major physical barriers. Nevertheless, numerous species reach either the northern or southern limits of their distributions between Colima and Guerrero. The Río Balsas apparently is a barrier to the dispersal of some species. Some of these *Cnemidophorus guttatus* in Guerrero, seemingly are replaced on the northwestern side of the river by another species that is an ecological replacement; in this case, *Cnemidophorus lineatissimus* in Michoacán is the ecological replacement of *C. guttatus* in Guerrero; *Leptodeira annulata* in Guerrero and southward is replaced by *Leptodeira maculata* in Michoacán and northward. Many species that are members of species groups or genera that are widely distributed in southern México and Central America occur on the coastal lowlands of Guerrero, but are unknown in Michoacán and northward on the coast. Species such as *Dermophis multiplicatus, Hyla staufferi, Ficimia publia, Leptophis mexicanus, Stenorrhina freminvillei,* and *Xenodon rhabdocephalus* are northern representatives of their respective groups and possibly are currently dispersing northward and have yet to reach Michoacán. It is noteworthy that the largest number of species on the lowlands is to the south, for only five species that do not occur in Michoacán are found on the lowlands of Colima and northward. All of these species have relatives to the south.

One of the most interesting and originally unsuspected distributional phenomena of the lowland fauna is the relatively high degree of faunal re-

semblance between the Tepalcatepec Valley and the coastal lowlands from Colima northward. An important dispersal route at the present time, and possibly even more important at the time of the Thermal Maximum, is the lowland passage from the Tepalcatepec Valley through the Ahuijullo depression to the lowlands of Colima. Duellman (1958) discussed this dispersal route as it pertained to the herpetofauna of Colima. *Hypsiglena torquata, Leptodeira latifasciata, Trimorphodon latifascia, Micrurus distans,* and *Micrurus laticollaris* are species that probably dispersed through the Ahuijullo depression when arid tropical scrub forest prevailed there, as it does now. At times when cooler climates prevailed and vegetation zones were altitudinally depressed, the low ridges between the Cordillera Volcánica and the Sierra de Coalcomán that form the Ahuijullo depression probably supported coniferous forest and consequently presented a barrier to the dispersal of lowland species through the depression. At times when broad-leafed deciduous forest or semi-deciduous forest existed in the depression, certain present foothill inhabitants, such as *Coniophanes lateritius, Leptodeira splendida,* and *Pseudoficimia frontalis* must have moved through the depression.

The steep rocky slopes in the narrow gorge of the lower Río Balsas seem to be a barrier to the dispersal of certain lowland species, such as *Rhinophrynus dorsalis, Crocodylus acutus, Dryadophis melanolomus,* and *Geagras redimitius.* Although many widespread lowland species do inhabit the gorge, I think that the Ahuijullo depression is a more important dispersal route than the Balsas gorge.

The large interior basin formed by the valleys of the Río Tepalcatepec and Río Balsas presents a rather uniform arid tropical environment, except that in the upper Balsas Basin in Morelos and Puebla conditions are more mesic than in the lower parts of the basin. The gradual disappearance of xeric-adapted species from the lower to upper parts of the basin reflects this gradual environmental change.

Certain minor dispersal routes exist between the lowlands and the Mexican Plateau. The most conspicuous of these routes are in western Jalisco, the upper Tepalcatepec Valley, the Tuxpan Valley, and the upper Balsas Basin (see discussion of these routes in the section on the Distribution of the Herpetofauna, page 685).

In southwestern México the major highland masses are the Sierra Madre Occidental, the Cordillera Volcánica, the Sierra de Coalcomán, and the Sierra Madre del Sur. In these mountains the altitudinal fluctuation in climate and vertical shifts in vegetation zones variously opened and closed different dispersal routes. At present the coniferous forests in the four ranges are isolated from one another by expanses of oak forest, mesquite-grassland, or tropical semi-deciduous forest, though possibly the coniferous forests in the Cordillera Volcánica are continuous with those in the Sierra Madre del Sur *via* the round-about route of the eastern part of the Cordillera Volcánica in Veracruz, southward through the Sierra Madre Oriental to the highlands of Oaxaca and then thence westward to the Sierra Madre del Sur in Guerrero.

Depression of environments in the Pleistocene must have permitted the growth of coniferous forest in the Ahuijullo depression and thereby provided a dispersal route for such montane species as *Bufo occidentalis, Eleutherodactylus augusti, Hyla bistincta, Sceloporus asper, Gerrhonotus imbricatus, Geophis petersi, Pituophis lineaticollis, Storeria storerioides, Thamnophis dorsalis,* a *Tomodactylus*-stock, and two *Geophis*-stocks. Some of these species possibly

entered the Sierra de Coalcomán from the Sierra Madre Occidental *via* the Ahuijullo depression. Probably *Sceloporus heterolepis* and *Sceloporus bulleri* arrived there from the Sierra Madre Occidental. Environments were not sufficiently depressed to permit the interchange of inhabitants of coniferous forest between the Sierra Madre del Sur and the Sierra de Coalcomán. Evidently a continuity of tropical semi-deciduous forest existed between the two ranges, for some species, such as *Microbatrachylus pygmaeus* and *Anolis dunni*, apparently entered the Sierra de Coalcomán from the Sierra Madre del Sur. The absence of such fir forest inhabitants as *Hyla lafrentzi, Sceloporus aeneus, Eumeces copei, Eumeces indubitus, Conopsis biserialis, Conopsis nasus, Tantilla bocourti,* and *Toluca lineata* in the Sierra de Coalcomán suggests that the depression of environments at the time of the Glacial Maximum was insufficient to allow the development of forests of cool pine and fir in the Ahuijullo depression and therefore did not provide a suitable environment for the dispersal of these species into the Sierra de Coalcomán.

Probably at the time of lowered vegetation zones a coniferous forest was continuous from the Sierra Madre Occidental throughout the Cordillera Volcánica to the Sierra Madre Oriental. The presence in all three ranges of such montane species as *Pseudoeurycea belli, Bufo occidentalis, Eleutherodactylus augusti, Sceloporus scalaris, Gerrhonotus imbricatus,* and *Toluca lineata* supports this hypothesis. However, climatic fluctuation served to separate and restrict the coniferous forests in these ranges, resulting in restricted distributions of certain species. For example, a major center of differentiation in salamanders of the genera *Chiropterotriton* and *Pseudoeurycea* seems to have been in the highlands of eastern México; no *Chiropterotriton* and only two species of *Pseudoeurycea* invaded the mountains to the west of the Valley of México. Contrariwise, none of the several species of *Tomodactylus* that apparently differentiated in the southwestern highlands reached the Sierra Madre Oriental.

Little, if any, interchange in the highland species seems to have taken place directly between the Cordillera Volcánica and the Sierra Madre del Sur. The latter has a herpetofauna composed of species either endemic to the area or distributed southward in the highlands of Oaxaca and in the Sierra Madre Oriental.

The herpetofauna of the southern part of the Mexican Plateau is composed primarily of wide-ranging components of the Desert and Plains Herpetofauna, and secondarily of species derived from the former. Except for a few species that apparently are recent invaders from the lowlands, the majority of species inhabiting the plateau probably arrived there from the north. The presence of the relictual populations of *Ambystoma dumerili, Rana dunni, Rana megapoda, Rana montezumae, Kinosternon hirtipes,* and *Thamnophis melanogaster,* all characteristic of aquatic and riparian habitats, indicates that mesic and pluvial conditions must have been more prevalent in postglacial times than at present.

Speciation in Southwestern México

Approximately 55 species of amphibians and reptiles are endemic to southwestern México. Of these, 13 are in the Balsas-Tepalcatepec Basin, five on the southern part of the Mexican Plateau, and 37 in the various mountain ranges. Available information concerning the phylogenies of the various

species, Pleistocene biogeography, and the known dispersal routes, provide clues as to the geographical and ecological factors that contributed to the isolation of populations that have subsequently differentiated. The following discussion pertains to the distributional phenomena involved in speciation in southwestern Mexico and is based on the premise that many species had similar geographic histories.

Of the 13 species endemic to the Balsas-Tepalcatepec Basin, seven (*Bufo perplexus, Hypopachus caprimimus, Bipes canaliculatus, Phyllodactylus duellmani, Phyllodactylus paucituberculatus, Urosaurus gadowi,* and *Leptotyphlops bressoni*) are inland vicariants of coastal species that do not inhabit the basin. Three other species apparently differentiated in the basin from coastal populations that reinvaded the basin after the inland populations had differentiated; the inland species and their respective parental species are *Sceloporus gadowae* and *S. pyrocephalus, Leptotyphlops gadowi* and *L. phenops,* and *Pseudoficimia pulcherrima* and *P. frontalis. Cnemidophorus calidipes* apparently differentiated in the Tepalcatepec Valley from a stock that also gave rise to *Cnemidophorus parvisocius* in the upper Balsas Basin. The two remaining endemics are relicts. *Enyaliosaurus clarki* is widely separated from its closest relative, *E. defensor* in the Yucatan Peninsula, although an apparently more distantly related species, *E. quinquccarinatus,* occurs on the Plains of Tehuantepec. Likewise, *Eumeces altamirani* is widely separated from its only Middle American relative, *E. schwartzei,* which is restricted to the Yucatan Peninsula. The present distributions and geographical histories of these two species cannot be explained, but the other endemics in the Balsas-Tepalcatepec Basin seemingly differentiated there from stocks of coastal species that invaded the basin. Possibly those endemics that occur sympatrically in the basin with their ancestral species became isolated there at an earlier time than were those species whose coastal relatives do not occur in the basin. Subspecific, as opposed to specific differentiation in the basin from coastal populations has occurred in three species of *Cnemidophorus—costatus, deppei,* and *lineatissimus.*

Of the five species endemic to the southern part of the Mexican Plateau, four are restricted to the aquatic and riparian habitats. *Ambystoma dumerili* apparently is a relict. *Rana dunni, R. megapoda,* and *R. montezumae,* all members of the widespread *R. pipiens* complex, are closely related, and their ranges are partly sympatric. Apparently they differentiated through isolation in different drainage basins on the southern part of the plateau. The information on each of these species suggests that formerly pluvial conditions were much more widespread than at present. *Lampropeltis ruthveni,* a member of the widespread *Lampropeltis doliata* group, apparently differentiated through isolation from an earlier *L. doliata* stock. At present *L. ruthveni* and *L. doliata* are sympatric on the southern part of the Mexican Plateau.

The vertical shifts in climate and vegetation in the high mountains of southwestern México in Pleistocene and postglacial times have resulted in migrations and isolation of many populations of various animal stocks. Often this isolation and subsequent differentiation have resulted in the formation of species pairs on isolated mountain ranges. For example, in the Sierra de Coalcomán *Geophis incomptus* and *G. nigrocinctus* are members of different species pairs that in the Sierra de los Tarascos are represented by *G. maculiferus* and *G. tarascae,* respectively. The *Tomodactylus angustidigitorum* group is represented by *T. angustidigitorum* in the Sierra de los Tarascos, *T. fuscus* in the Sierra de Temazcaltepec, and *T. grandis* in the Sierra Ajusco, whereas the *T. dilatus*

group inhabits the other major mountain masses in southwestern México with *T. dilatus* in the Sierra Madre del Sur and *T. rufescens* in the Sierra de Coalcomán.

The greatest amount of differentiation has taken place in the Sierra Madre del Sur. Nineteen species are endemic to that mountain mass, which forms the northern extension of the highlands of southern México. Apparently differentiation has occurred there through isolation primarily from southern stocks.

SUMMARY

1.—Michoacán is made up of five physiographic regions: Pacific Coastal Plain, Balsas-Tepalcatepec Basin, Mexican Plateau, Cordillera Volcánica, and Sierra de Coalcomán.

2.—The Balsas-Tepalcatepec Basin, a structural depression, formerly was connected to the Pacific Coastal Plain *via* the Ahuijullo depression. The two major highland masses in the state had independent histories.

3.—The lowlands are characterized by high temperatures and seasonal rainfall; the Mexican Plateau likewise receives rainfall which is highly seasonal and scanty, but the temperatures on the plateau are moderate. Low temperatures and moderate amounts of precipitation characterize the higher mountains, where snow falls in winter.

4.—The major vegetation types and animal habitats in the state are: Fir forest (2400-4000 meters), pine-oak forest (1000-4000 meters), mesquite-grassland (1500-2100 meters), arid tropical scrub forest (0-1000 meters), and tropical semi-deciduous forest (150-600 meters).

5.—The probable total herpetofauna of the state of Michoacán consists of 185 species and subspecies, but the occurrence of nine of these in the state is hypothetical.

6.—A definite correlation exists between the major animal habitats and the distribution of amphibians and reptiles in the state. Upper and lower limits of altitudinal distribution usually are associated with noticeable ecological changes at the same elevations.

7.—The principal factors affecting the ecological distributions of amphibians and reptiles apparently are: presence or absence of certain microhabitats, reproductive habits of the animals, diel activities of the animals, and ecological segregation.

8.—The ecological-geographical concepts of biomes, life zones, and biotic provinces are inadequate for the analysis of the distribution of amphibians and reptiles in southwestern México. Instead, a method of ascertaining faunal resemblance is employed.

9.—Three major herpetofaunal assemblages are recognized in southwestern México — Neotropical (three subdivisions), Sierra Madrean (five subdivisions), and Desert and Plains. Each is characterized by different assemblages of species.

10.—Ecological factors are important in limiting local distributions of amphibians and reptiles in southwestern México, but the broad basic distributional patterns are closely correlated with physiography.

11.—Four major elements are present in the herpetofauna in southwestern México—South American Element, Old Northern Element (Central American Complex), Middle American Element, and Young Northern Element (Madrean Complex and Desert and Plains Complex). Each element has had a different geographic history.

12.—In the establishment of present patterns of distribution the most important factors are the climatic and corresponding altitudinal fluctuations in the Pleistocene and postglacial times.

13.—Major lowland dispersal routes in southwestern México are the Pacific Coastal Plain and the passage through the Ahuijullo depression between the Balsas-Tepalcatepec Basin and the lowlands of Colima. A major highland route at times of depression of environments was through the Ahuijullo depression between the Cordillera Volcánica and Sierra de Coalcomán.

14.—Although some endemic relicts are present in the herpetofauna in southwestern México, most endemic species there apparently originated *in situ*. Species pairs in various mountain ranges are the result of dispersal of stocks and subsequent isolation in the mountains.

LITERATURE CITED

Axelrod, D. I.
1958. Evolution of the Madro-Tertiary Geoflora. Botanical Rev., 24:433-509.

Axtell, R. W.
1962. Can we use biotic provinces? Systematic Zool., 11:93-96.

Blair, W. F.
1958. Distributional patterns of vetebrates in the southern United States in relation to past and present environments. Zoogeography. Amer. Assoc. Advanc. Sci., Publ. No. 51:433-468.

Blásquez, L. and Garcia, P. L.
1946. Hidrogeología y minerales no-metalicos de la zona norte del Estado de Michoacán. Anal. Inst. Geol., 9:1-156.

Brand, D. D.
1957. Coastal study of southwest Mexico, Part I. Univ. Texas, Austin, xii + 140 pp.
1958. Coastal study of southwest Mexico, Part II. Univ. Texas, Austin, vii + 279 pp.

Brand, D. D. and others
1960. Coalcomán and Motines del Oro. Univ. Texas, Austin, xx + 403.

Burt, W. H.
1949. Present distribution and affinities of Mexican mammals. Ann. Assoc. Amer. Geog., 39:211-218.
1958. The history and affinities of the Recent land mammals of western North America. Zoogeography. Amer. Assoc. Advanc. Sci., Publ. No. 51:131-154.
1961. Some effects of Volcán Parícutin on vertebrates. Occ. Papers Mus. Zool. Univ. Michigan, 620:1-22, pls. 1-2.

Carr, A. F.
1950. Outline for a classification of animal habitats in Honduras. Bull. Amer. Mus. Nat. Hist., 94:563-594.

Carreño, A.
1943. El volcán de Parícutin en las primeras fases de su erupción. Irrigación en México, 24:49-80.

Clements, F. E. and Shelford, V. E.
1939. Bioecology. John Wiley and Sons, New York, 425 pp.

Clisby, K. H. and Sears, P. B.
1956. San Augustine Plains—Pleistocene climatic changes. Science, 124:537-539.

Contreras Arias, A.
1942. Mapa de las provincias climatologias de la República Mexicana. Dir. Geog., Meter., Hidrol., México, xxviii pp., 54 tables, 2 maps.

Darlington, P. J.
1957. Zoogeography: The geographical distribution of animals. John Wiley and Sons, New York, xi + 675 pp.

Davis, W. B., and Dixon, J. R.
1959. Snakes of the Chilpancingo Region, Mexico. Proc. Biol. Soc. Washington, 72:79-92.
1961. Reptiles (exclusive of snakes) of the Chilpancingo Region, Mexico. Proc. Biol. Soc. Washington, 74:37-56.

Davis, W. B. and Smith, H. M.
1953a. Snakes of the Mexican state of Morelos. Herpetologica, 8:133-143.
1953b. Amphibians of the Mexican state of Morelos. Herpetologica, 8: 144-149.

1953c. Lizards and turtles of the Mexican state of Morelos. Herpetologica, 9:100-108.

DEEVEY, E. S. and FLINT, R. F.
1957. Postglacial hypsithermal interval. Science, 125:182-184.

DETERRA, H., ROMERO, J., and STEWARD, T. D.
1949. Tepexpan Man. Viking Fund Publ. in Anthropology, 11:1-160, 37 pls.

DICE, L. R.
1943. The biotic provinces of North America. Univ. Michigan Press, Ann Arbor, vii + 78 pp.

DORF, E.
1959. Climatic changes in the past and present. Contr. Mus. Paleo. Univ. Michigan, 13:181-210, 1 pl.

DUELLMAN, W. E.
1958. A preliminary analysis of the herpetofauna of Colima, Mexico. Occ. Papers Mus. Zool. Univ. Michigan, 589:1-22.
1960a. Variation, distribution, and ecology of the Mexican teiid lizard *Cnemidophorus calidipes*. Copeia, 2:97-101.
1960b. A distributional study of the amphibians of the Isthmus of Tehuantepec, México. Univ. Kansas Publ. Mus. Nat. Hist., 13-19-72, pls. 1-8.
1961. The amphibians and reptiles of Michoacán, México. Univ. Kansas Publ. Mus. Nat. Hist., 15:1-148, pls. 1-6.
1963. Amphibians and reptiles of the rainforests of southern El Petén, Guatemala. Univ. Kansas Publ. Mus. Nat. Hist., 15:205-249, pls. 7-10.

DUNN, E. R.
1931. The herpetological fauna of the Americas. Copeia, 3:106-119.

FIRSCHEIN, I. L. and SMITH, H. M.
1956. A new fringe-limbed *Hyla* (Amphibia: Anura) from a new faunal district of Mexico. Herpetologica, 12:17-21.

FLINT, R. F.
1957. Glacial and Pleistocene geology. John Wiley and Sons, New York, xiii + 553 pp.

FLORES, T.
1946. Geología minera de la region NE del Estado de Michoacán. Bull. Inst. Geol., 56:1-106.

GARFIAS, V. R. and CHAPIN, T. C.
1949. Geología de México. México, 202 pp.

GENTRY, H. S.
1942. Rio Mayo plants. Carnegie Inst. Washington, Publ. 527: vii + 328 pp.

GLENDENING, GEORGE E.
1952. Some quantitative data on the increase of mesquite and cactus on a desert grassland range in southern Arizona. Ecology, 33:319-328.

GLOYD, H. K.
1940. The rattlesnakes, genera *Sistrurus* and *Crotalus*. Chicago Acad. Sci. Spec. Publ., 4:vii + 266 pp., 31 pls.

GOLDMAN, E. A.
1951. Biological investigations in Mexico. Smithsonian Miscel. Coll., 115:xiii + 476 pp.

GOLDMAN, E. A. and MOORE, R. T.
1946. The biotic provinces of Mexico. Jour. Mammalogy, 26:347-360.

Harding, G.
1960. The competitive exclusion principle. Science, 131:1292-1297.

Hershkovitz, P.
1958. A geographic classification of Neotropical Mammals. Fieldiana. Zool., 36:581-620.

Hevly, R. H. and Martin, P. S.
1961. Geochronology of Pluvial Lake Cochise, southern Arizona. I. Pollen analysis of shore deposits. Jour. Arizona Acad. Sci., 2:24-31.

Hibbard, C. S.
1960. An interpretation of Pliocene and Pleistocene climates in North America. 62nd Annual Rept. Michigan Acad. Sci. Arts, Lett., pp. 5-30.

Hutchinson, G. E., Patrick, R., and Deevey, E. S.
1956. Sediments of Lake Patzcuaro, Michoacan, Mexico. Bull. Geol. Soc. Amer., 67:1491-1504.

Humphrey, R. R. and Mehrhoff, L. A.
1958. Vegetation changes on a southern Arizona grassland range. Ecology, 39:720-726.

Imlay, R. W.
1944. Cretaceous formations of the Greater Antilles, Central America, and Mexico. Bull. Geol. Soc. America, 55:1005-1046.

Johnson, D. H., Bryant, M. D., and Miller, A. H.
1948. Vertebrate animals of the Providence Mountains area of California. Univ. California Publ. Zool., 48:221-376.

Kendeigh, S. C.
1954. History and evaluation of various concepts of plant and animal communities in North America. Ecology, 35:152-171.
1961. Animal Ecology. Prentice-Hall, Englewood Cliffs, x + 468 pp.

Leavenworth, W. C.
1946. A preliminary study of the vegetation of the region between Cerro Tancitaro and the Rio Tepalcatepec, Michoacan, Mexico. Amer. Midl. Nat., 36:137-206.

Leopold, A. S.
1950. Vegetation zones of Mexico. Ecology, 31:507-518.

Long, C. A.
1963. Mathematical formulas expressing faunal resemblance. Trans. Kansas Acad. Sci., 66:138-140.

Martin, P. S.
1958a. A biogeography of reptiles and amphibians in the Gomez Farias region, Tamaulipas, Mexico. Misc. Publ. Mus. Zool. Univ. Michigan, 101:1-102.
1958b. Pleistocene ecology and biogeography of North America. Zoogeography. Amer. Assoc. Advanc. Sci., Publ. No. 51:375-420.

Martin, P. S. and Harrell, B. E.
1957. The Pleistocene history of Temperate biotas in Mexico and eastern United States. Ecology, 38:468-480.

Martin, P. S., Robins, C. R., and Heed, W. B.
1954. Birds and biogeography of the Sierra de Tamaulipas, an isolated pine-oak forest. Wilson Bulletin, 60:38-57.

Martin, P. S., Schoenwetter, J., and Arms, B. C.
1961. The last 10,000 years. Geochronology Lab., Univ. Arizona, vi + 119 pp., 14 pls.

Matthew, W. D.
1915. Climate and evolution. Ann. New York Acad. Sci., 24:171-318.

MERRIAM, C. H.
1890. Results of a biological survey of the San Francisco mountain region and desert of the Little Colorado in Arizona. North Amer. Fauna, No. 3:1-136.
1894. Laws of temperature control of the geographic distribution of terrestrial animals and plants. Nat. Geog. Mag., 6:229-238.

MILLER, A. H.
1951. An analysis of the distribution of the birds of California. Univ. California Publ. Zool., 50:531-644.

MIRANDA, F.
1952. La vegetación de Chiapas, Part I. Dept. Prensa y Turismo, Tuxtla Gutierrez, 334 pp.

MOORE, R. T.
1945. The transverse volcanic biotic province of central Mexico and its relationship to adjacent provinces. Trans. San Diego Soc. Nat. Hist., 10:217-236.

MULLER, C. H.
1939. Relations of the vegetation and climatic types in Nuevo León, Mexico. Amer. Midl. Nat., 21:687-729.
1947. Vegetation and climate of Coahuila, Mexico. Madroño, 9:33-57.

ORDÓÑEZ, E.
1941. Las provincias fisiográficas de México. Rev. Geog. Inst. Panamer. Geog. y Hist., 1:133-181.

PETERS, J. A.
1955. Use and misuse of the biotic province concept. Amer. Nat., 89: 21-28.

PIRLOT, P. L.
1956. Les formes européene du genre *Hipparion*. Inst. Geol. Barcelona, Mem. y Comun., 14:1-150.

POTZGER, J. E. and THARP, B. C.
1947. Pollen profile from a Texas bog. Ecology, 28:274-280.
1954. Pollen study of two bogs in Texas. Ecology, 35:462-466.

RABB, G. B.
1958. On certain Mexican salamanders of the plethodontid genus *Chiropterotriton*. Occ. Papers Mus. Zool. Univ. Michigan, 587:1-37.

ROBLES, R. R.
1942. Orgénesis de la República Mexicana. Irrigación en México, 23:7-61.

RUTHVEN, A. G.
1908. Variation and genetic relationships of the garter-snakes. Bull. U. S. Natl. Mus., 61:1-201.

SAVAGE, J. M.
1960. Evolution of a peninsular herpetofauna. Systematic Zool., 9:184-212.

SCHMIDT, K. P.
1943. Corollary and commentary for "Climate and evolution." Amer. Midl. Nat., 30:241-253.

SCHUCHERT, C.
1935. Historical geology of the Antillean-Caribbean region. New York, xxvi + 811 pp.

SEARS, P. B., FOREMAN, F., and CLISBY, H. K.
1955. Palynology in southern North America. Bull. Geol. Soc. Amer., 66:471-530.

Sharp, A. J.
1946. Informe preliminár sobre algunos estudios fitogeográficos efectuados en México y Guatemala. Rev. Soc. Mexicana Hist. Nat., 7:35-40.

Simpson, G. G.
1943. Turtles and the origin of the fauna of Latin America. Amer. Jour. Sci., 241:413-429.
1953. Evolution and geography. Eugene, Oregon, 64 pp.
1960. Notes on the measurement of faunal resemblance. Amer. Jour. Sci., 258A:300-311.

Smith, H. M.
1939. The Mexican and Central American lizards of the genus *Sceloporus*. Zool. Ser. Field Mus. Nat. Hist., 26:1-397.
1940. An analysis of the biotic provinces of Mexico, as indicated by the distribution of the lizards of the genus *Sceloporus*. Anal. Esc. Nac. Cien. Biol., 2:95-110.
1949. Herpetogeny in Mexico and Guatemala. Ann. Assoc. Amer. Geog., 39:219-238.
1960. An evaluation of the biotic province concept. Systematic Zool., 9:41-44.

Smith, H. M., and Taylor, E. H.
1945. An annotated checklist and key to the snakes of Mexico. Bull. U. S. Natl. Mus., 187:iv + 239 pp.
1948. An annotated checklist and key to the Amphibia of Mexico. Bull. U. S. Natl. Mus., 194:iv + 118 pp.
1950. An annotated checklist and key to the reptiles of Mexico exclusive of the snakes. Bull. U. S. Natl. Mus., 199:v + 253 pp.

Storm, M.
1939. Hoofways into hot country. Bland Bros., Mexico City, 521 pp.

Stuart, L. C.
1932. Studies on Neotropical Colubrinae. I. The taxonomic status of the genus *Drymobius* Fitzinger. Occ. Papers Mus. Zool. Univ. Michigan, 236:1-16, 5 pls.
1943. Taxonomic and geographic comments on Guatemalan salamanders of the genus *Oedipus*. Misc. Publ. Mus. Zool. Univ. Michigan, 56:1-32.
1950. A geographical study of the herpetofauna of Alta Verapaz, Guatemala. Contr. Lab. Vert. Biol., Univ. Michigan, 45:1-77, 9 pls.
1957. Herpetofaunal routes through northern Central America. Copeia, 2:89-94.

Swadley, W. C.
1958. Mineralology of the beach sands of Michoacán, Mexico. *in* Brand, D. D., Coastal study of southwest Mexico, Part II. Univ. Texas, Austin, pp. 187-210.

Tamayo, J. L.
1941. Morfología de la República Mexicana y división regional de la misma. Rev. Geog. Inst. Panamer. Geog. y Hist., 1:221-235.
1949. Geografía general de México. I. Geografía fisica. Mexico City, viii + 628 pp.

Thayer, W. N.
1916. The physiography of Mexico. Jour. Geol., 24:61-94.

Vestal, A. G.
1914. Internal relations of terrestrial associations. Amer. Nat., 48:413-445.

Vivo, J.
1953. Geografía de México. Mexico City, ed. 3, 338 pp.

WHITE, S. E.
1956. Probable substages of glaciation on Ixtaccihuatl, Mexico. Jour. Geology, 64:289-295.

WILLIAMS, H.
1950. Volcanoes of the Parícutin region, Mexico. Geol. Surv. Bull., 965-B:165-279.

ZWEIFEL, R. G.
1960. A new species of lizard (genus *Cnemidophorus*) from Mexico. Amer. Mus. Novitates, 1998:1-8.

Transmitted July 27, 1965,

□

30-8425

(Continued from inside of front cover)

Vol. 13. 1. Five natural hybrid combinations in minnows (Cyprinidae). By Frank B. Cross and W. L. Minckley. Pp. 1-18. June 1, 1960.
2. A distributional study of the amphibians of the Isthmus of Tehuantepec, México. By William E. Duellman. Pp. 19-72, pls. 1-8, 3 figures in text. August 16, 1960. 50 cents.
3. A new subspecies of the slider turtle (Pseudemys scripta) from Coahuila, México. By John M. Legler. Pp. 73-84, pls. 9-12, 3 figures in text. August 16, 1960.
°4. Autecology of the copperhead. By Henry S. Fitch. Pp. 85-288, pls. 13-20, 26 figures in text. November 30, 1960.
5. Occurrence of the garter snake, Thamnophis sirtalis, in the Great Plains and Rocky Mountains. By Henry S. Fitch and T. Paul Maslin. Pp. 289-308, 4 figures in text. February 10, 1961.
6. Fishes of the Wakarusa River in Kansas. By James E. Deacon and Artie L. Metcalf. Pp. 309-322, 1 figure in text. February 10, 1961.
7. Geographic variation in the North American cyprinid fish, Hybopsis gracilis. By Leonard J. Olund and Frank B. Cross. Pp. 323-348, pls. 21-24, 2 figures in text. February 10, 1961.
8. Descriptions of two species of frogs, genus Ptychohyla; studies of American hylid frogs, V. By William E. Duellman. Pp. 349-357, pl. 25, 2 figures in text. April 27, 1961.
9. Fish populations, following a drought, in the Neosho and Marais des Cygnes rivers of Kansas. By James Everett Deacon. Pp. 359-427, pls. 26-30, 3 figures. August 11, 1961. 75 cents.
10. North American recent soft-shelled turtles (family Trionychidae). By Robert G. Webb. Pp. 429-611, pls. 31-54, 24 figures in text. February 16, 1962. $2.00.

Index. Pp. 613-624.

Vol. 14. 1. Neotropical bats from western México. By Sydney Anderson. Pp. 1-8. October 24, 1960.
2. Geographic variation in the harvest mouse, Reithrodontomys megalotis, on the central Great Plains and in adjacent regions. By J. Knox Jones, Jr., and B. Mursaloglu. Pp. 9-27, 1 figure in text. July 24, 1961.
3. Mammals of Mesa Verde National Park, Colorado. By Sydney Anderson. Pp. 29-67, pls. 1 and 2, 3 figures in text. July 24, 1961.
4. A new subspecies of the black myotis (bat) from eastern Mexico. By E. Raymond Hall and Ticul Alvarez. Pp. 69-72, 1 figure in text. December 29, 1961.
5. North American yellow bats, "Dasypterus," and a list of the named kinds of the genus Lasiurus Gray. By E. Raymond Hall and J. Knox Jones, Jr. Pp. 73-98, 4 figures in text. December 29, 1961.
6. Natural history of the brush mouse (Peromyscus boylii) in Kansas with description of a new subspecies. By Charles A. Long. Pp. 99-110, 1 figure in text. December 29, 1961.
7. Taxonomic status of some mice of the Peromyscus boylii group in eastern Mexico, with description of a new subspecies. By Ticul Alvarez. Pp. 111-120, 1 figure in text. December 29, 1961.
8. A new subspecies of ground squirrel (Spermophilus spilosoma) from Tamaulipas, Mexico. By Ticul Alvarez. Pp. 121-124. March 7, 1962.
9. Taxonomic status of the free-tailed bat, Tadarida yucatanica Miller. By J. Knox Jones, Jr., and Ticul Alvarez. Pp. 125-133, 1 figure in text. March 7, 1962.
10. A new doglike carnivore, genus Cynarctus, from the Clarendonian Pliocene, of Texas. By E. Raymond Hall and Walter W. Dalquest. Pp. 135-138, 2 figures in text. April 30, 1962.
11. A new subspecies of wood rat (Neotoma) from northeastern Mexico. By Ticul Alvarez. Pp. 139-143. April 30, 1962.
12. Noteworthy mammals from Sinaloa, Mexico. By J. Knox Jones, Jr., Ticul Alvarez, and M. Raymond Lee. Pp. 145-159, 1 figure in text. May 18, 1962.
13. A new bat (Myotis) from Mexico. By E. Raymond Hall. Pp. 161-164, 1 figure in text. May 21, 1962.
°14. The mammals of Veracruz. By E. Raymond Hall and Walter W. Dalquest. Pp. 165-362, 2 figures in text. May 20, 1963. $2.00.
15. The Recent mammals of Tamaulipas, México. By Ticul Alvarez. Pp. 363-473, 5 figures in text. May 20, 1963. $1.00.
16. A new subspecies of the fruit-eating bat, Sturnira ludovici, from western Mexico. By J. Knox Jones, Jr., and Gary L. Phillips. Pp. 475-481, 1 figure in text. March 2, 1964.
17. Records of the fossil mammal Sinclairella, Family Apatemyidae, from the Chadronian and Orellan. By William A. Clemens, Jr. Pp. 483-491, 2 figures in text. March 2, 1964.
18. The mammals of Wyoming. By Charles A. Long. Pp. 493-758, 82 figures in text. July 6, 1965. $3.00.

Index. Pp. 759-784.

(Continued on outside of back cover)

(Continued from inside of back cover)

Vol. 15. 1. The amphibians and reptiles of Michoacán, México. By William E. Duellman. Pp. 1-148, pls. 1-6, 11 figures in text. December 20, 1961. $1.50.
2. Some reptiles and amphibians from Korea. By Robert G. Webb, J. Knox Jones, Jr., and George W. Byers. Pp. 149-173. January 31, 1962.
3. A new species of frog (genus Tomodactylus) from western México. By Robert G. Webb. Pp. 175-181, 1 figure in text. March 7, 1962.
4. Type specimens of amphibians and reptiles in the Museum of Natural History, The University of Kansas. By William E. Duellman and Barbara Berg. Pp. 183-204. October 26, 1962.
5. Amphibians and reptiles of the rainforests of southern El Petén, Guatemala. By William E. Duellman. Pp. 205-249, pls. 7-10, 6 figures in text. October 4, 1963.
6. A revision on snakes of the genus Conophis (Family Colubridae, from Middle America). By John Wellman. Pp. 251-295, 9 figures in text. October 4, 1963.
7. A review of the Middle American tree frogs of the genus Ptychohyla. By William E. Duellman. Pp. 297-349, pls. 11-18, 7 figures in text. October 18, 1963. 50 cents.
8. Natural history of the racer Coluber constrictor. By Henry S. Fitch. Pp. 351-468, pls. 19-22, 20 figures in text. December 30, 1963. $1.00.
9. A review of the frogs of the Hyla bistincta group. By William E. Duellman. Pp. 469-491, 4 figures in text. March 2, 1964.
10. An ecological study of the garter snake, Thamnophis sirtalis. By Henry S. Fitch. Pp. 493-564, pls. 23-25, 14 figures in text. May 17, 1965.
11. Breeding cycle in the ground skink, Lygosoma laterale. By Henry S. Fitch and Harry W. Greene. Pp. 565-575, 3 figures in text. May 17, 1965.
12. Amphibians and reptiles from the Yucatan Peninsula, México. By William E. Duellman. Pp. 577-614, 1 figure in text. June 22, 1965.
13. A new species of turtle, genus Kinosternon, from Central America. By John M. Legler. Pp. 615-625, pls. 26-28, 2 figures in text. July 20, 1965.
14. A biogeographic account of the herpetofauna of Michoacán, México. By William E. Duellman. Pp. 627-709, pls. 29-36, 5 figures in text. December 30, 1965.

More numbers will appear in volume 15.

Vol. 16. 1. Distribution and taxonomy of mammals of Nebraska. By J. Knox Jones, Jr. Pp. 1-356, plates 1-4, 82 figures in text. October 1, 1964. $3.50.
2. Synopsis of the lagomorphs and rodents of Korea. By J. Knox Jones, Jr., and David H. Johnson. Pp. 357-407. February 12, 1965.
3. Mammals from Isla Cozumel, Mexico, with description of a new species of harvest mouse. By J. Knox Jones, Jr., and Timothy E. Lawlor. Pp. 409-419, 1 figure in text. April 13, 1965.
4. The Yucatan deer mouse, Peromyscus yucatanicus. By Timothy E. Lawlor. Pp. 421-438, 2 figures in text. July 20, 1965.

More numbers will appear in volume 16.

Vol. 17. 1. Localities of fossil vertebrates obtained from the Niobrara Formation (Cretaceous) of Kansas. By David Bardack. Pp. 1-14. January 22, 1965.
2. Chorda tympani branch of the facial nerve in the middle ear of tetrapods. By Richard C. Fox. Pp. 15-21. June 22, 1965.

More numbers will appear in volume 17.

S-NH-L[awrence]

University of Kansas Publications
Museum of Natural History

Volume 15, No. 15, pp. 711-744, pls. 37, 38, 6 figs.
March 7, 1966

MUS. COMP. ZOOL
LIBRARY
JUN 15 1966
HARVARD
UNIVERSITY

Amphibians and Reptiles of Mesa Verde National Park, Colorado

BY

CHARLES L. DOUGLAS

University of Kansas
Lawrence
1966

UNIVERSITY OF KANSAS PUBLICATIONS
MUSEUM OF NATURAL HISTORY

Institutional libraries interested in publications exchange may obtain this series by addressing the Exchange Librarian, University of Kansas Library, Lawrence, Kansas. Copies for individuals, persons working in a particular field of study, may be obtained by addressing instead the Museum of Natural History, University of Kansas, Lawrence, Kansas. When individuals request copies from the Museum, 25 cents should be included, for each 100 pages or part thereof, for the purpose of defraying the costs of wrapping and mailing. For certain longer papers an additional amount, indicated below, toward some of the costs of production, is to be included.

° An asterisk designates those numbers of which the Museum's supply is exhausted.

Vol. 1. Nos. 1-26 and index. Pp. 1-638, 1946-1950.

°Vol. 2. (Complete) Mammals of Washington. By Walter W. Dalquest. Pp. 1-444, 140 figures in text. April 9, 1948.

Vol. 3. °1. The avifauna of Micronesia, its origin, evolution, and distribution. By Rollin H. Baker. Pp. 1-359, 16 figures in text. June 12, 1951.
°2. A quantitative study of the nocturnal migration of birds. By George H. Lowery, Jr. Pp. 361-472, 47 figures in text. June 29, 1951.
3. Phylogeny of the waxwings and allied birds. By M. Dale Arvey. Pp. 473-530, 49 figures in text, 13 tables. October 10, 1951.
°4. Birds from the state of Veracruz, Mexico. By George H. Lowery, Jr., and Walter W. Dalquest. Pp. 531-649, 7 figures in text, 2 tables. October 10, 1951.
Index. Pp. 651-681.

°Vol. 4. (Complete) American weasels. By E. Raymond Hall. Pp. 1-466, 41 plates, 31 figures in text. December 27, 1951.

Vol. 5. Nos. 1-37 and index. Pp. 1-676, 1951-1953.

°Vol. 6. (Complete) Mammals of Utah, *taxonomy and distribution.* By Stephen D. Durrant. Pp. 1-549, 91 figures in text, 30 tables. August 10, 1952.

Vol. 7. Nos. 1-15 and index. Pp. 1-651, 1952-1955.

Vol. 8. Nos. 1-10 and index. Pp. 1-675, 1954-1956.

Vol. 9. Nos. 1-23 and index. Pp. 1-690, 1955-1960.

Vol. 10. Nos. 1-10 and index. Pp. 1-626, 1956-1960.

Vol. 11. Nos. 1-10 and index. Pp. 1-703, 1958-1960.

Vol. 12. °1. Functional morphology of three bats: Eumops, Myotis, Macrotus. By Terry A. Vaughan. Pp. 1-153, 4 plates, 24 figures in text. July 8, 1959.
°2. The ancestry of modern Amphibia: a review of the evidence. By Theodore H. Eaton, Jr. Pp. 155-180, 10 figures in text. July 10, 1959.
3. The baculum in microtine rodents. By Sydney Anderson. Pp. 181-216, 49 figures in text. February 19, 1960.
°4. A new order of fishlike Amphibia from the Pennsylvanian of Kansas. By Theodore H. Eaton, Jr., and Peggy Lou Stewart. Pp. 217-240, 12 figures in text. May 2, 1960.
5. Natural history of the Bell Vireo, Vireo bellii Audubon. By Jon C. Barlow. Pp. 241-296, 6 figures in text. March 7, 1962.
6. Two new pelycosaurs from the lower Permian of Oklahoma. By Richard C. Fox. Pp. 297-307, 6 figures in text. May 21, 1962.
7. Vertebrates from the barrier island of Tamaulipas, México. By Robert K. Selander, Richard F. Johnston, B. J. Wilks, and Gerald G. Raun. Pp. 309-345, pls. 5-8. June 18, 1962.
8. Teeth of edestid sharks. By Theodore H. Eaton, Jr. Pp. 347-362, 10 figures in text. October 1, 1962.
9. Variation in the muscles and nerves of the leg in two genera of grouse (Tympanuchus and Pedioecetes) By E. Bruce Holmes. Pp. 363-474, 20 figures in text. October 25, 1963. $1.00.
10. A new genus of Pennsylvanian fish (Crossopterygii, Coelacanthiformes) from Kansas. By Joan Echols. Pp. 475-501, 7 figures in text. October 25, 1963.
11. Observations on the Mississippi kite in southwestern Kansas. By Henry S. Fitch. Pp. 503-519. October 25, 1963.
12. Jaw musculature of the Mourning and White-winged doves. By Robert L. Merz. Pp. 521-551, 22 figures in text. October 25, 1963.
13. Thoracic and coracoid arteries in two families of birds, Columbidae and Hirundinidae. By Marion Anne Jenkinson. Pp. 553-573, 7 figures in text. March 2, 1964.
14. The breeding birds of Kansas. By Richard F. Johnston. Pp. 575-655, 10 figures in text. May 18, 1964. 75 cents.
15. The adductor muscles of the jaw in some primitive reptiles. By Richard C. Fox. Pp. 657-680, 11 figures in text. May 18, 1964.
Index. Pp. 681-694.

(Continued on inside of back cover)

University of Kansas Publications
Museum of Natural History

Vol. 15, No. 15, pp. 711-744, pls. 37, 38, 6 figs.
March 7, 1966

Amphibians and Reptiles of Mesa Verde National Park, Colorado

BY

CHARLES L. DOUGLAS

University of Kansas
Lawrence
1966

S-NA-L[awrence]

UNIVERSITY OF KANSAS PUBLICATIONS, MUSEUM OF NATURAL HISTORY

Editors: E. Raymond Hall, Chairman, Henry S. Fitch,
Frank B. Cross

Volume 15, No. 15, pp. 711-744, pls. 37, 38, 6 figs.
Published March 7, 1966

MUS. COMP. ZOOL.
LIBRARY

JUN 15 1966

HARVARD
UNIVERSITY

UNIVERSITY OF KANSAS
Lawrence, Kansas

PRINTED BY
ROBERT R. (BOB) SANDERS, STATE PRINTER
TOPEKA, KANSAS
1966

30-8424

Amphibians and Reptiles of Mesa Verde National Park, Colorado

BY

CHARLES L. DOUGLAS

INTRODUCTION

Mesa Verde National Park is in the Four Corners region of southwestern Colorado, northeast of the place where the boundaries of Utah, Colorado, New Mexico and Arizona meet at a common junction. The park was set aside in 1906, and now more than 51,000 acres are included in order to protect cliff dwellings built by prehistoric Pueblo Indians.

Geologically Mesa Verde consists of Cretaceous strata of coal-bearing sandstone termed the Mesaverde Group. The dip is from north to south and the resultant drainage is southward into the Mancos River. Erosion has dissected the plateau into large finger-like mesas, united at their northern ends but otherwise separated by deep canyons. Southward in the park the bottoms of these canyons are 600 to 900 feet below the tops of the mesas; as a consequence, the landscape of Mesa Verde is exceedingly rugged. As one approaches the park from the east, its north rim towers 1500 feet above the surrounding Montezuma Valley. The plateau tilts to the south and loses 1500 feet in elevation within ten miles. The southern ends of the mesas are about 6300 feet in elevation, but are still 900 feet higher than the Mancos River that has cut a deep canyon along the southern ends of the mesas, separating them from the tableland to the south.

The climate of Mesa Verde is semiarid; annual precipitation has averaged 18.45 inches over the last 40 years. July and August generally have the most rain. The nearby La Plata Mountains influence the climate of the park; orographic storms originate there and reach the higher elevations of the mesas first. As a consequence, the higher, northern parts of the park receive more yearly precipitation than the southern end. Summer rains tend to be highly localized, often affecting only a part of one mesa at a time.

Mesa Verde is in the pinyon-juniper woodland biome of Shelford, and the Navahonian biotic province of Dice (Dice, 1962). According to Cary (1911:34) the top of the mesa is in the Transition Life-zone of Merriam. Actually most of the vegetation on the mesa top is

pinyon-juniper woodland and therefore in the Upper Sonoran Life-zone. Canyons support tall sagebrush (*Artemisia tridentata*) and rabbitbrush (*Chrysothamnus nauseosus*) in their sandy bottoms, while mixed shrubs (*Cerococarpus, Sarcobatus, Fendlera, Amelanchier*) grow on the talus slopes. Sagebrush is also found on the mesa tops, generally as a late successional stage in areas disturbed by fire. Sagebrush is common near prehistoric dwellings, on trash mounds and on surface sites where the soil is friable and suitable for its growth.

Douglas fir (*Pseudotsuga menziesii*) is found on cool, north-facing slopes, in moist canyons such as Spruce Tree Canyon, and especially along the slopes on the northern escarpment of the park. Relict stands of ponderosa pine in a few sheltered canyons represent the Transition Life-zone. Oak thickets occur along the northern edge of mesas, on slopes of canyons and along drainages. The vegetation of the park is largely that of the Upper Sonoran Life-zone; vegetation of the Transition Life-zone is restricted to suitable microenvironments along sheltered north-facing slopes or in cool canyons.

The prehistoric Pueblos were the culmination of a culture that had occupied the Mesa Verde region since the sixth century. The most primitive of the inhabitants were termed Basketmakers, since they made baskets but no pottery; theirs was largely a hunting and gathering society. They lived in simple shelters called pit houses, raised some crops and began to domesticate the wild turkey. The Basketmaker culture gradually evolved into a pottery making one with more dependence upon agriculture. Rudimentary pit houses evolved into masonry rooms and kivas (underground rooms with circular walls). The Pueblo period of this culture was reached around 1100 A. D. with the construction of majestic stone buildings both on the mesas and in natural cavelike depressions in the sandstone cliffs. Many of the black and white items of pottery made by these Pueblos are objects of great beauty. The exterior of some bowls bear forms of animals contemporaneous with the prehistoric Indians. Even then people were intrigued by the grotesque horned lizard, and silhouettes of it are not uncommon on pottery.

After occupying Mesa Verde for about 700 years, the Indians left in about A. D. 1300 and migrated south into more favorable areas. Tree rings from timbers in the ruins and from the oldest trees in the park indicate extended periods of poor tree growth prior to abandonment. These narrow tree rings have been interpreted as indicating twenty years of drought. Drought and extended periods

of poor crops could have led to eventual migration from the Mesa Verde region.

In 1959 the Wetherill Mesa Archeological Project was organized as part of Mission 66. One objective of that Mission was to extend facilities of the national park system to meet the needs of increasing numbers of visitors. The Wetherill Mesa Project was organized to excavate and prepare for visitor-use the cliff and surface sites on Wetherill Mesa. Such excavation involves systematic unearthing, detailed observations, and extensive collections in order to extract maximum information from an archeological site. In order that as much as possible might be learned about the lives of the prehistoric Indians, the National Geographic Society annually contributed funds to support scientific investigations ancillary to the archeological investigation proper.

In 1961 I joined the staff of the Wetherill Mesa Project, as biologist. After mummified lizards and snake vertebrae were found in the ruins, I decided to collect reptiles, as time permitted, in order to learn what kinds were present and how they were distributed in the park.

In some phases of my study, for instance in preparing Figs. 3, 4, and 5, some specimens obtained immediately outside the boundary of the park on the southern ends of Chapin or Moccasin Mesas (Fig. 1) have been used. This was done because some species are more abundant just outside the boundary than within, and represent the same population of reptiles. Any such specimens so used are listed beyond in the accounts of species under a heading *"Some specimens examined from outside the National Park."* Small (6-point) type is used for this listing. Localities for specimens in several museum collections, including the park's collection, are labeled and/or listed in catalogues as Soda Tip-Off Trail, Mesa Verde National Park, although this locality is outside the park boundary.

The first reptile collected in the park was a specimen taken by Merritt Cary in 1907; the specimen is now in the United States National Museum and was mentioned by Cary in his Biological Survey of Colorado (Cary, 1911:26). Specimens taken by Lewis T. Barry in the early 1930s also are in the National Museum. The museum at the park has specimens taken by C. W. Quaintance in the 1930s, and later by Don Watson, who was Park Naturalist. Specimens in the University of Kansas Museum of Natural History were collected by Sydney Anderson in 1956 while he was studying the mammals of the park (Anderson, 1961), or by myself. From July

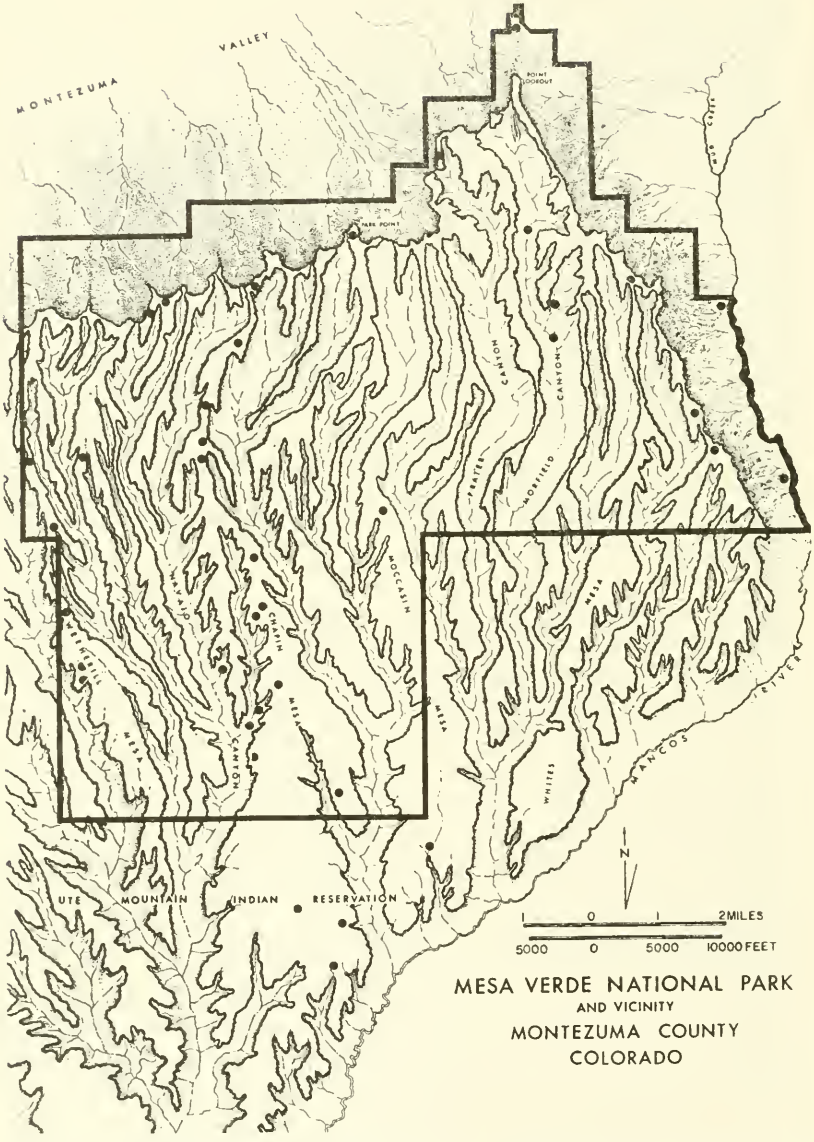


FIG. 1. Map of Mesa Verde National Park and vicinity, showing localities where amphibians or reptiles were collected in the period 1962-1964. Localities within ¼ mile of each other are not indicated by separated dots.

1961 to August 1964 I spent 28 months in residence at the park, and collected 279 specimens of amphibians and reptiles. Three hundred ten specimens were examined from the park proper. The total number of specimens examined is 466.

The names of museums containing specimens examined from Mesa Verde National Park are abbreviated as follows:

American Museum Natural History—AMNH
Brigham Young University—BYU
University of Colorado—CU
The University of Kansas—KU
Mesa Verde National Park—MVNP
Museum of Vertebrate Zoology, Univ. California, Berkeley—MVZ
United States National Museum—USNM
University of Utah—UU

Specimens bearing numbers 373 through 820, with no prefix, are in my collection; the majority of these specimens will be placed in the University of Kansas Museum of Natural History. Specimens in the park's museum do not have catalogue numbers, and when there is more than one specimen represented the number of specimens is in parentheses.

For assistance and encouragement in the course of my study, I am grateful to Dr. Laurence M. Klauber, Dr. William E. Duellman, Dr. Hobart M. Smith, Mr. Bob Reese and Mr. Charles J. Cole for assistance in identifying specimens. Several persons assisted me in the field, especially Mrs. Marilyn Colyer and John G. Douglas. Mr. Bill Burnett captured several fine specimens of rattlesnakes, and his assistance is especially appreciated. Food items were identified by Marilyn Colyer. Dr. John A. Davidson identified ticks and mites. The endoparasites were determined by Mr. John Ubelaker. Mrs. Pauline Goff and Marilyn Colyer assisted with preparation of specimens in the laboratory and with organizing data. Professor E. Raymond Hall, Professor Hobart M. Smith, Mr. Jerry Downhower, and Mr. Richard Holland reviewed the manuscript and offered suggestions for its improvement. Professors H. M. Smith and T. Paul Maslin were especially helpful in making available the records of Mesa Verde specimens housed in various museums, as well as data to be published in their study of the herpetofauna of Colorado.

A special note of thanks is due Mrs. Jean Pinkley, Chief of Interpretation, and Dr. Douglas Osborne, Supervisory Archeologist of the Wetherill Mesa Archeological Project, for their encouragement throughout this study.

The Wetherill Mesa Project is a part of the research program of the National Park Service locally supported in part by the National

Geographic Society, to which I am indebted for a major share of the support that resulted in this report. This is Contribution No. 36 of the Wetherill Mesa Archeological Project.

ACCOUNTS OF SPECIES

Ambystoma tigrinum utahense Lowe

Utah Tiger Salamander

Specimens examined.—Total, 4: ¼ mi. S Entrance, 7000 ft., 457-459, 638.

Salamanders were in a cisternlike enclosure protecting valves regulating water flow to the residence at the park entrance. This cement-walled enclosure extends about five feet into the ground; drainage from a nearby water tank and leakage from the control valves causes several inches of water to stand in the bottom of the enclosure throughout spring and summer. Salamanders burrow into the resulting mud, and also tunnel around the pipes leading into and from the enclosure. Apparently there is access to the outside from within the enclosure, for a captive salamander defecated several large grasshopper legs, indicating that at least this individual fed on the large number of grasshoppers nearby.

Salamanders have been observed, by members of the ranger staff, in similar enclosures used for garbage at the residence at the entrance to the park. The garbage bins were dry and did not contain salamanders when I inspected them.

One specimen was emaciated and obviously near starvation when captured (Fig. 2). Its left mandibular ramus has been broken and extends forward (anteriorly and laterally) beyond the front of the skull. The broken end of the ramus is healed and covered with skin. Individuals of *Ambystoma* are known to fight over food when

Fig. 2. Ventral view of a specimen (No. 452 CLD) of *Ambystoma tigrinum utahense* in which the left mandibular ramus is broken, and projects anteriorly and laterally. The broken place in the jaw is healed and covered with skin. The injury was probably caused by fighting. × 1.

kept in captivity, and such activity probably explains the injury in this specimen.

Ambystoma has probably ventured into the park from the Mancos River by way of Mud Creek. During the rainy season of July and

August, salamanders could easily journey from the drainages of Mud Creek and into the area of the entrance station. The members of this genus are known for their migratory abilities. Salamanders were not observed in the Mancos River, but a more thorough search would probably reveal their presence there.

Large numbers of larval salamanders were seen in August 1964 by Bob Reese in a pond beside Highway 160, about two miles west of Mancos, Colorado. The Mancos River lies approximately midway between the Mancos locality (a man-made pond) and the park locality (also man-made). Salamanders can obviously survive in the Montezuma Valley, in spite of the semiarid nature of the region. In Mesa Verde proper, they are restricted by lack of available habitat.

Bufo punctatus Baird and Girard

Red-spotted Toad

Specimens examined.—Total 3: Mesa Verde National Park, MVNP.

Other records.—Mesa Verde National Park, AMNH 6931, CU 7524; Mesa Verde National Park, 6200 ft., MVZ 22359; Park Headquarters, CU 5590.

Some specimens examined from outside the National Park.—Bedrock drainage, 200 yds. N 16 Window House, S. Chapin Mesa, 673-674.

Runoff water has sculptured large depressions in the sandstone floor of small drainages on the southern end of Chapin Mesa. In one such drainage, large pot holes contain water for much of the summer, and especially during the rainy parts of late July and August. Water persists in the largest pot holes until late autumn. These are the only spots on the mesa top in which red-spotted toads were found to lay their eggs.

The pot holes have steep, bowllike sides, and several inches of silt in the bottom. Larger depressions are approximately four feet in diameter and two and one-half feet deep. The depth of the water appears to fluctuate from zero in early summer to about two feet in August through October. Numerous mosquito larvae and small crustaceans lived in the water; water striders were present on the surface. Water plants were not present, as such, but adjacent grasses and cattails had roots extending into the water of the largest pot hole. Algae were abundant on the sides of the depression, and the water had a greenish cast.

Recently-hatched tadpoles, one-half inch long, were collected on 2 August 1963. By mid-August the tadpoles were beginning to develop legs, and by 6 October, they had metamorphosed and were found deep in the grass beside the largest pot holes. The young toads averaged about fifteen millimeters in snout-vent length. Even these small animals were brightly marked with the characteristic

red dots on a larger black spot. The tail was completely absorbed, and the posterior portions of the thighs appeared translucent and unpigmented. Only one adult toad was found; it was inadvertently caught in a snake trap that was placed beside a vertical face of rock in the bottom of the drainage. The toad was completely dessicated when found a day or two later; it had been skeletonized by ants and beetles that were still in the trap.

The insect fauna of this particular drainage is varied and abundant. Lizards of several species (*Sceloporus undulatus, S. graciosus, Urosaurus ornatus, Uta stansburiana* and *Crotaphytus collaris*) also occur there.

Bufo woodhousei woodhousei Girard

Rocky Mountain Toad

Specimens examined.—Total 2: Prater Canyon, 7500 ft., MVNP; Prater Canyon, 7600 ft., MVNP.

Bufo woodhousei is known in the park only from Prater Canyon. The specimens probably came from in or near the old wells in the bottom of the canyon. Inspection of the wells several times in the summer of 1963 revealed no sign of toads. The species probably occurs in the riparian habitats along the Mancos River.

Rana pipiens brachycephala Cope

Western Leopard Frog

Specimens examined.—Total 3: W. side of Mancos River, 4¾ mi. SE Point Lookout, 612; W. side of Mancos River, 4½ mi. SE Point Lookout, 620; Mancos River near Weber Canyon, MVNP.

Leopard frogs are common along the banks of the Mancos River, which forms the eastern boundary of the park. This is the only permanent body of water within the park, and consequently is the only locality where these frogs were found.

Terrapene ornata ornata (Agassiz)

Ornate Box Turtle

The box turtle is a resident of the eastern plains of Colorado, but recently has been introduced into the park by summer visitors, and will probably establish itself there. I have frequently seen box turtles along US 160 between the park and Durango, Colorado. Tourists apparently pick up the turtles on the eastern side of the mountains, become tired of them later, and then drop them at the first opportunity.

In the summer of 1963, a park employee found four box turtles in a garbage can in Campground No. 3. They were given to the daughters of Mr. and Mrs. A. Hewitt, and were kept in a pen until they eventually escaped. On 29 August 1963 I picked up a medium sized box turtle on the road near Campground No. 3. It may have been one of the turtles that escaped from the Hewitt girls, or, perhaps another that had been brought into the park by visitors.

This animal ate voraciously while in captivity, but escaped after two months and was not seen again. I see no reason why these turtles could not survive in Mesa Verde, since they are already acclimated to hot, dry summers and cold winters of the eastern plains.

Crotaphytus collaris auriceps Fitch and Tanner

Yellow-headed Collared Lizard

Specimens examined.—Total 5: Rock Ledge above Ruin No. 16, 7125 ft., Wetherill Mesa, 469, 471; Wetherill Lab, 7200 ft., Chapin Mesa, 563; Spruce Tree Canyon, CU 4462-4463.

Additional Records.—Mesa Verde National Park, BYU 498-878 (1 specimen).

The collared lizard was seen along rocky ledges above cliffs, on talus slopes and occasionally in bottoms of canyons. Specimens from Mesa Verde were discussed in the original description of this subspecies (Fitch and Tanner, 1951:556).

A captive collared lizard readily ate adult scelopori, taking from one-half to one hour to swallow the prey. The strong jaws of the collared lizard can inflict painful bites and once a hold is secured on another lizard, the meal has literally begun. Lizards of the genus *Sceloporus* were generally swallowed head first, although several were swallowed tail first.

This species is not uncommon within the park, but like other predatory animals, is less abundant than its prey, and is seen proportionately fewer times. When adults are found, they are often pugnacious and stand their ground, making capture easier.

Specimen No. 471, an adult male, had dozens of small nematodes, *Pharyngodon giganticus*, in his intestines. Remains of arthropods were present in the stomach of this specimen.

Holbrookia maculata approximans Baird

Speckled Earless Lizard

A specimen examined from outside the National Park.—Mancos River Valley, USNM 88608.

Only one specimen of *Holbrookia* has been recorded for Mesa Verde. It was obtained in 1933 by Don Watson, then the park

naturalist, and was presented to Lewis T. Barry at the Colorado Museum of Natural History (Barry, 1933) who reported that Watson saw another near Park Headquarters.

Other specimens of this species have been taken from Montezuma County (Barry, 1932, 1933; Maslin, 1959). A specimen of *H. m. approximans* (USNM 88608) was obtained by Barry in the "Mancos River Valley." Montezuma County is the only county in Colorado where *H. m. approximans* has been found; *H. m. maculata* is relatively well distributed in the state (Maslin, 1959:28; H. M. Smith and T. P. Maslin, R. L. Brown, 1965). I spent many hours in each of several summers unsuccessfully searching for this species in the park. I can only conclude that it is no longer a park resident.

Sceloporus graciosus graciosus Baird and Girard

Great Basin Sagebrush Lizard

Specimens examined.—Total 163: N. end Morfield Canyon, 373; Wetherill Lab, 7200 ft., Chapin Mesa, KU 80648, KU 80651, 730, 755-756, 764-765; Wetherill Mesa Camp, 7125 ft., 389; Cliff above Mug House, Wetherill Mesa, 390; Rock Springs, Wetherill Mesa, 391, 578-582; Cabin, Whites Mesa, 7645 ft., KU 80649; Morfield Canyon, 7300 ft., 395; M2 Weather Station, 7200 ft., Chapin Mesa, 418, KU 80653-80654, 460-462, 464-465, 508-510, 767-768; Spruce Tree Canyon, Chapin Mesa, 423-424; 1 mi. S, ¼ mi. E Morfield Well, Morfield Canyon, 7550 ft., 476; 1.7 mi. S Morfield Well, 7350 ft., Morfield Canyon, 477-478; Spruce Canyon, 503; 4.5 mi. S North Rim, 7450 ft., Moccasin Mesa, 525-526; Station 6, 4 mi. S North Rim, 7525 ft., Moccasin Mesa, 528-530; Reservoir site 1073, 4.4 mi. S North Rim, Moccasin Mesa, 531; 2.2 mi. S Wetherill Road, 7975 ft., Long Mesa, 598; Wetherill Road, 8220 ft., ½ mi. E Long Mesa Road, 599; Knife Edge, 8200 ft., 609-611; 3¾ mi. E, 5¾ mi. S Point Lookout, 6275 ft., 621-623; Log Cabin, Campground No. 1, 7000 ft., Chapin Mesa, 625, 652; Big Mesa, 5½ mi. S, 2¾ mi. E Point Lookout, 7525 ft., 626; Big Mesa, 5 mi. S, 2¾ mi. E Point Lookout, 7725 ft., 627; ⅜ mi. N C2 Weather Station, N. Navajo Canyon, 635; Sun Tower, CU 4539-4540; S. end Chapin Mesa, CU 4541-4572; Weber Canyon, 6200 ft., CU 5592; Mesa Verde National Park, CU 9431-9432, KU 16834; Jct. Ute and Frink Trails, 8113 ft., KU 51492; Rock Springs, 7400 ft., KU 51493-51501, KU 51503-51504, KU 51506, KU 51509-51511; Mancos River, 6200 ft., KU 51505; 1 mi. NNW Rock Springs, 7600 ft., KU 51507-51508; ½ mi. NNW Rock Springs, 7500 ft., KU 51512-51513; Museum, MVNP; N. Rim above Prater Canyon, MVNP; Chapin Mesa, 7100 ft., MVNP; Chapin Mesa, 7000 ft., MVNP; Spruce Tree Canyon, USNM 88596-88597.

Additional Records.—Mesa Verde National Park, BYU 11927-869, BYU 11928-881, MVZ 40767, UU 970-972.

Some specimens examined from outside the National Park.—S. Tip Chapin Mesa, 6500 ft., 387, KU 80650; Soda Canyon Tip-Off Trail, and rocks above, S. Chapin Mesa, 515, 519, 747-748; Sage Flat, S. Chapin Mesa, KU 80652; Rock outcroppings and bedrock drainage, 10 mi. S North Rim, Moccasin Mesa, 547-562, 567, 570, 773-777.

The sagebrush lizard is probably the most abundant lizard of the Mesa Verde. Of all park lizards, this species is most nearly ubiquitous, yet it may be seen less frequently by the casual visitor to the area than is *S. undulatus*. Visitors to the park enter cliff dwellings by means of trails along cliffs where *S. undulatus* is most abundant. *S. graciosus* may be seen along such trails, and may even be found

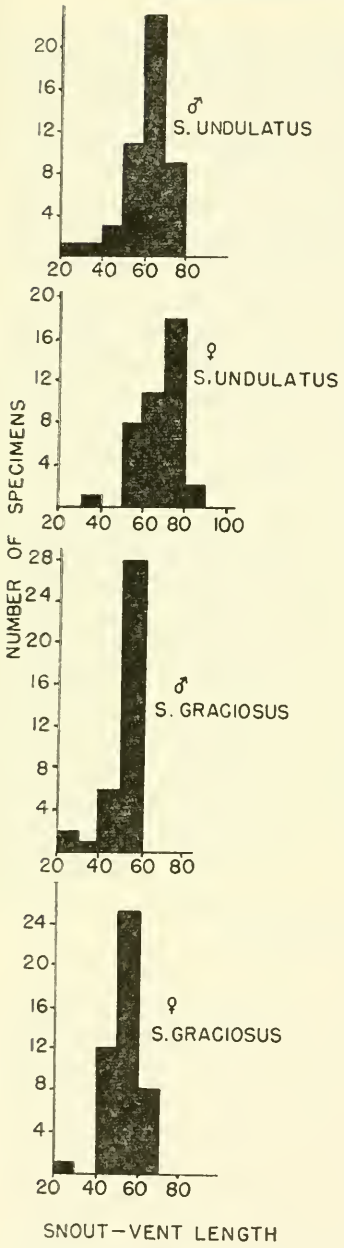


FIG. 3. Size groups of two species of lizards, *Sceloporus undulatus* and *S. graciosus*, showing differences in specimens collected in 1963-1964. Females of each species attain longer bodies than males.

sunning side by side with *undulatus*. But, *S. graciosus* is more common in pinyon-juniper associations, and areas with dense growths of brush. Shade and concomitantly lower temperatures appear to be necessary requirements for the sagebrush lizard. No specimens were taken from open, rocky areas after the sun had heated the rocks to even a moderate extent. Conversely, fence lizards were often collected from rocks that had been warmed considerably. Harris (1963: 21) observed a dependence of *S. graciosus* upon shade in the San Juan Basin, New Mexico, and noted that this lizard is active for longer periods of the day than most. Gehlbach (1965:257) also considers partial shade to be a niche requirement for *S. graciosus* in northwestern New Mexico. Darker coloration and smaller size of *S. graciosus* probably permit more rapid warming by insolation than do the paler coloration and larger size of *S. undulatus*. As the angle of insolation decreases in late afternoon, larger lizards may not be able to stay sufficiently warm to remain active, and therefore retire. *S. graciosus* probably requires absorption of less reradiated heat to warm his body, and can therefore remain active longer in the day.

Specimens were taken from pinyon-juniper associations, from bedrock drainages next to stands of pinyon-juniper or ponderosa pine; beside buildings surrounded by pinyon-juniper woodland; in canyon bottoms having Douglas fir or pinyon-juniper associations; from forest edges adjacent to sagebrush flats; on

rocks near the edges of cliffs; from boulders in oak thickets (*Quercus gambelii*) along the northern rim of the mesas; and from elevations of 6300 to 8500 feet. *S. graciosus* but not *S. undulatus* was taken in the 1959 Morfield Burn that currently supports dense growths of grasses and low thickets of oak brush. Only one sagebrush lizard was taken from a relatively pure stand of sagebrush (*Artemisia tridentata*), a vegetational cover under which there are high surface temperatures and relatively little shade. It is interesting to note that Gehlbach (1965:257) found *S. graciosus* only in the vicinity of big sagebrush or saltbrush, on loose soil. This was not the preferred habitat in Mesa Verde, but a difference in ground cover could be as important as the overstory vegetation. Specimens were taken from the northern and southern escarpments of the park, from sites along the eastern and western edges, and from numerous mesa and canyon localities between the extreme elevations.

Figure 3 shows the relative sizes of 37 male and 47 female lizards collected in 1963-1964. Of these, body lengths of 26 adult males and 30 adult females were essentially equal (52 and 54 millimeters, respectively; $s = 4.3 — 4.9$). Tails averaged longer in the males (73 mm.— $s = 6.3$ as opposed to 68 mm.— $s = 9.7$), than in females (Fig. 4). The largest lizards in the population were old females, which attain larger bodies and longer tails than the largest males.

In 62 specimens of both sexes there is an average of 26 femoral pores (range 22-30; $s = 2.8$); pores in the male are the larger, more obvious, and have well-developed glandlike functions as evidenced by extrusions of waxy material. Pores in the female appear almost vestigial; except in a few specimens, waxy material is not extruded by the pores. The secondary sexual difference in pores is evident in the breeding season as well as at other times.

Gravid females were collected from 21 May through 8 July. *S. graciosus* is known to lay from two to seven eggs in early July (Smith, 1946:250). Ova in the specimens collected in May were about five by seven millimeters. By late June, other specimens had ova seven by thirteen millimeters. A gravid female on 8 July contained six large eggs, the largest of which was eight by fourteen millimeters. Seven females contained from three to seven eggs each (ave. 4.7). Four large eggs averaging 8.1 by 13.2 mm. from a female caught on 8 July 1963 contained well-developed embryos. They were in a stage of development analagous to the head fold—tail bud stage in the chicken.

Young of the year were first observed on 8 August 1963, when the snout-vent length of one was 26 mm. and its tail was 31. Two

young, (625, 626) collected on 11 September 1963 had snout-vent lengths of 27 and 28 millimeters.

About 86 percent of the specimens of *S. graciosus* are heavily parasitized by chiggers (*Trombicula a. alfreddugesi* Oudemans), in the axillary and cloacal regions. Mites, *Geckobiella texana* (Banks), were found on several specimens. The nematode *Pharyngodon giganticus* was common in intestinal tracts of the park lizards; only one specimen contained a tapeworm (*Oochoristica* sp.).

S. graciosus eats a large variety of arthropods and other animals, depending upon kinds that are most abundant. Ants seem to be a preferred food; Knowlton (1946) reports that of 1239 stomachs of *S. graciosus* examined, 631 contained a total of 7470 ants (see, also, Smith, 1946:251; Stebbins, 1954:246; Knowlton, 1942, 1946, 1947, 1948, 1953). Stomachs of eight specimens from Mesa Verde contained the following families and genera of arthropods:

Rhinotermitidae (termites)
Miridea, *Halictus* sp. (leaf bugs)
Cicadellidae (leafhoppers)
Carabidae (ground beetles)
Tenebrionidae (darkling beetles)
Chrysomelidae (leafhopper beetles)
Curculionidae (snout beetles)
Scarabaeidae (dung beetles)
Phyllophaga (June beetles)
Coccinellidae, *Hippodamia* (lady bug)
Lepidoptera (butterflies and moths)
Cyclorrhapha (circular seamed flies)
Orthorrhapha (straight seamed flies)
Rhagionidae (snipe fly)
Formicidae
Campanotus vicinus
Lasius niger neoniger
Crematogaster lineolata
Araneida, Lycosidae
Pseudoscorpion

An adult *S. graciosus* was found in the stomach of a *Masticophis taeniatus,* that had been hit on the park road. Captive individuals of *Pituophis, Thamnophis* and *Crotaphytus* also ate adult *S. graciosus* lizards.

Sceloporus undulatus elongatus Stejneger
Northern Plateau Lizard

Specimens examined.—Total 176: Cliffs above Swallow's Nest, 6775 ft., Chapin Mesa, KU 80655, 604-607; N. Navajo Canyon, near C2 Weather Station, KU 80669; Spruce Tree Canyon, Chapin Mesa, KU 80670-80672; M2 Weather Station, 7200 ft., Chapin Mesa, 463, 507, 790; 1 mi. S, ¼ mi. E Morfield Well, Morfield Canyon, 7550 ft., 473-475; ¼ mi. S Far View Ruins, 7600 ft., Chapin Mesa, 479; Spruce Canyon, 504-505; 4.5 mi. S North Rim, Moccasin Mesa, 7450 ft., 524; Wetherill Road, ½ mi. E of head W. Navajo Canyon, 7975 ft., 602-603; Knife Edge, 8200 ft., 608; Rocks of drainage, ¼ mi. E Soda Tip-Off Trail, S. Chapin Mesa, 629-630; ⅜ mi. N C2 Weather Station, North Navajo Canyon, 6500 ft., 636-637; Long House trail, Wetherill Mesa, 639-642, 651; Rocks above Little Long House, Chapin Mesa, 653-654; Trail to Spruce Tree House, 700, 707; Sun Tower, CU 4716-4722; S. end Chapin Mesa, CU 4723-4755; Mancos River side canyon, 6400 ft., CU 5593-5598; Near Hemenway House, CU 18648; Rock Springs, 7400 ft., KU 51502; ½ mi. NNW Rock Springs, 7500 ft., KU 51514; Wickiup Canyon, MVNP; Mancos River, 6400 ft., MVNP; Mesa Verde National Park, USNM 88584-88591.

Additional Records.—Spruce and Navajo Canyons, AMNH 13608-13613; Chapin Mesa, AMNH 13619-13622; Mesa Verde National Park, 6500 ft., MVZ 22373.

Some specimens examined from outside the National Park.—S. tip Chapin Mesa, 6500 ft., KU 80656-80658, KU 80666; Soda Canyon Tip-Off Trail, Chapin Mesa, 520, 613-616, 741-746, 757-758, KU 80659-80660, KU 80677 (2 specimens), MVNP; Drainage 100 yds. W of gravel pit, S. Chapin Mesa, 466, 489-496, 511-514, 719-720, 734-738, 761, KU 80661-80665, KU 80667-80668, KU 80673-80676, KU 80678-80684; Rock outcroppings and bedrock drainage, 10 mi. S of North Rim, Moccasin Mesa, 536-546, 565-566, 571, 769-772; Southern tip Moccasin Mesa, cliffs and drainages, 779-781.

Sceloporus undulatus occurs in several habitats in Mesa Verde; rocky terrain including boulders and edges of cliffs appears to be favored. Due to the diversity of habitats occupied by this species, its distribution overlaps that of several other species of lizards within the park. The plateau lizard often suns upon the same boulder as, and feeds in close proximity to, *Sceloporus graciosus*, *Urosaurus ornatus* and *Uta stansburiana*. This compatibility, or tolerance between species within the same habitat, apparently reflects differences in food habits and other requirements of their respective niches. The plateau lizard is found in suitable habitats from the northern escarpment of the park to the southern edges of the mesas.

Specimens were taken in the following places: pinyon-juniper woodland; from bedrock drainages adjacent to stands of pinyon-juniper, ponderosa pine or Douglas fir; along sandstone cliffs bordered by various associations of vegetation; in trees; on rocks in thickets of scrub oak (*Quercus gambelii*) along the northern extremities of the mesas; around buildings, and from boulders in canyon bottoms. This species was not taken from sagebrush flats or from the 1959 Morfield Burn (an area encompassing more than 2000 acres on Morfield Mesa, Whites Mesa and the surrounding canyons, which burned in July of 1959) that currently supports grasses and low thickets of oak brush. Availability of rocks appears to be more important for this lizard than does the nature of the adjacent vegetation. Harris (1963:20) found the species in similar habitats in New Mexico.

Figure 3 shows the size distribution of 49 male and 41 female lizards collected in their periods of activity in 1963-1964. Of these, thirty-five adult males had an average body length of 63 millimeters ($s = 7$) and 30 adult females an average of 67 mm. ($s = 8.6$) for body length. Tails were longer in females than in males; means were 94 and 91 mm. ($s = 9.6$ and 9.4) for females and males, respectively. Females thereby tend to be slightly longer than males; and the largest females are noticeably longer than the longest males (Fig. 5).

Thirty-one adult males had a range of 32-41 femoral pores (ave. 37, $s = 4$); 30 females had a range of 31-40 (ave. 36, $s = 3$) femoral

pores. Waxy extrusions from the pores indicate them to be functional in both sexes, but more active in males.

The dark blue of the abdominal patches in the male appeared to be of the same intensity throughout the lizard's period of activity. If these patches become darker in the breeding season, it was not detectable in captives or in other specimens that I collected. Abdominal patches in females were consistently paler than those in males.

S. undulatus hibernates until the snow is completely gone and the ground is warm. The first scelopori were seen in 1962 on 11 April, although characteristic rustlings, that may have been lizards, were heard in leaves under oak brush on 1 April. In 1963, the first lizard was seen in Spruce Tree Canyon on March 31. The late snows and cold weather during the spring of 1964 kept these lizards in hibernation, or at least out of sight, until April 16.

In three successive springs (1962-1964) the hatching of insects preceded emergence from hibernation by lizards. For example, in 1962 flies were noticed on 1 April. The insect hatches had started by March 21 in 1963, and leafhoppers were among the first to appear. Winged beetles, sulfur moths, grasshoppers and flies appeared, in that order, within another day or two. In 1964, the first flies were seen on 28 March, although five to twelve inches of snow persisted in the woods. In each year the lizards appeared approximately ten to fifteen days after the hatching of the insects.

Hibernation of these lizards apparently begins by mid-September in Mesa Verde. On 16 September 1963 only two lizards were seen in an area that had had a high population of *S. undulatus* throughout the summer. Two lizards were collected along the trail to Spruce Tree House on 22 October, but no other lizards were seen until the following spring.

Young of the year were first observed in Navajo Canyon on 23 September 1963. One young female obtained on that date had a body length of 32 millimeters. Gravid females containing five to eight ova (average 6) were collected from June to early July. The largest ova, measuring 8 by 16 millimeters, were found in specimens on 27 June and 2 July. Smaller ova were found on 5 July and 5 August in other specimens—probably reflecting a long breeding season, and indicating that all females may not breed in the first part of the season. Some females may attempt a second clutch; a large female on 5 August contained eight small ova (each approximately 4 by 5 mm.). Ova this small, so late in the season,

probably could not have hatched successfully if they had been laid when mature; such ova likely would be retained over winter and laid in the following spring.

Heavy infestations of chiggers (*Trombicula a. alfreddugesi*) occurred around the vent and in the axillary and ear regions of 95 percent of the specimens. Mites (*Geckobiella texana*) were present on a few individuals. The presence of ectoparasites probably explains the scratching by a S. *undulatus* that I observed on 26 September 1963 while collecting along the Mug House trail. The lizard was sunning on a rock, and periodically scratched his axilla with one hind foot, in much the same manner as a dog.

The following orders, families and genera of arthropods were represented in stomach contents of five lizards:

Cicadellidae (leafhoppers)
Tenebrionidae (darkling beetles)
Chrysomelidae (leafhopper beetles)
Curculionidae (snout beetles)
Scarabaeidae (dung beetles)
Phyllophaga (June beetles)
Lepidoptera (butterflies and moths)
Scoliidae (digger wasps)
Vespidae (yellow jackets)
Tachinidae (tachinid flies)
Tiphiidae (tiphiids)
Tipulidae (crane flies)
Formicidae
Campanotus vicinus
Lasius niger neoniger
Crematogaster lineolata

Intestinal parasites were common; nematodes (*Pharyngodon giganticus*) and tapeworms (*Oochoristica bivitellolobata*) were found.

A *Masticophis taeniatus* found dead on the park road contained a small adult S. *undulatus*. This species of lizard was offered at intervals as a food item to captive garter snakes and gopher snakes. Both species of snakes ate adult lizards when hungry, but otherwise ignored them. Plateau lizards probably are eaten by *Crotaphytus collaris;* a captive *Crotaphytus* ate adult scelopori with ease.

Urosaurus ornatus wrighti (Schmidt)
Northern Tree Lizard

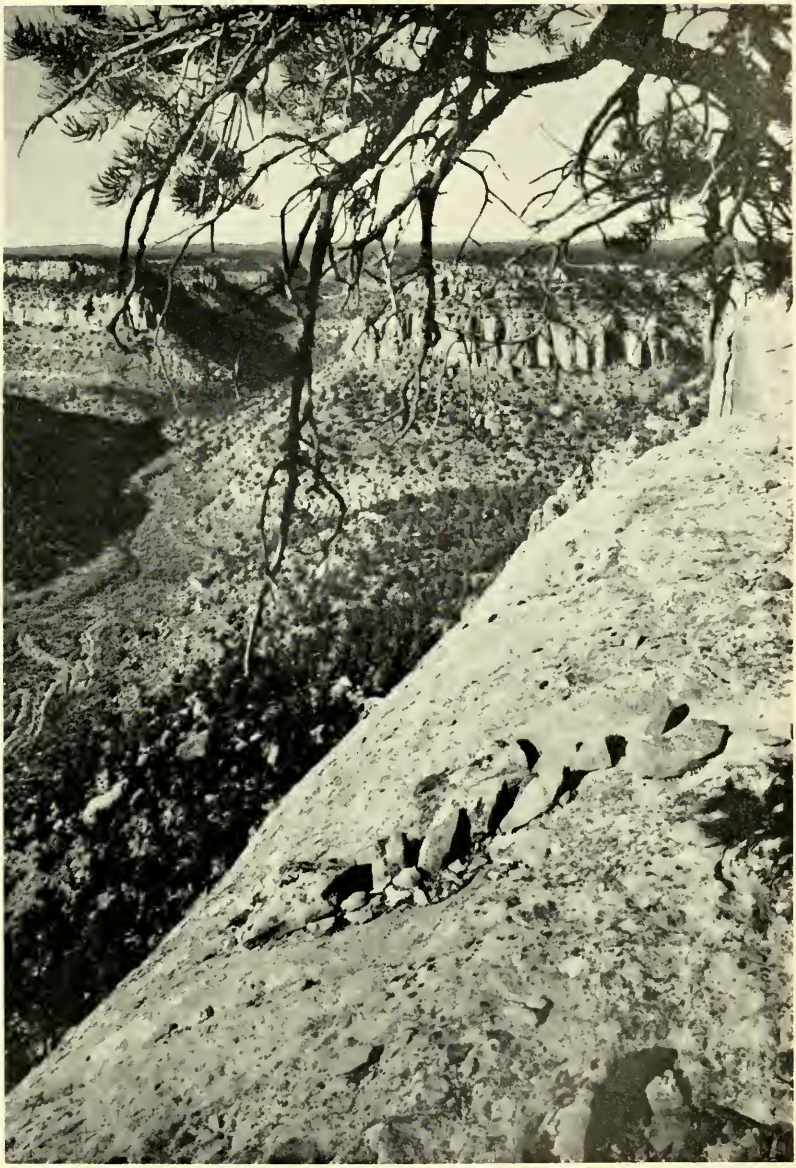
Specimens examined.—Total 35: Rocks above Little Long House, Chapin Mesa 655; Mesa Verde National Park, KU 16885-16886, USNM 40186; Mancos River side canyon (2) MVNP; Rim rock of Prater Canyon, above Chickaree Draw, 8000 ft., MVNP.

Additional Records.—Mesa Verde National Park, BYU 612-873, BYU 1652-2268, BYU 1653-864, BYU 1650-866, UU 974-975; S. end Chapin Mesa, CU 4838-4842; E. Rock Canyon, 7200 ft., CU 5594.

Some specimens examined from outside the National Park.—Soda Canyon Tip-Off Trail, S. Chapin Mesa, 396, 516, 759-760 (1), MVNP; Drainage 100 yds. W of gravel pit, S. Chapin Mesa, 402-405, 411, 430-431, 442-443, 487, 739-740, 762; Rock outcroppings and bedrock drainage, 10 mi. S of North Rim Moccasin Mesa, 532-535, 568-569, 778; Southern tip Moccasin Mesa, cliffs and drainages, 782-784.

Urosaurus ornatus is restricted in habitat to boulders, cliffs and canyon walls (Mittleman, 1942; Smith, 1946:275). The species frequently was seen on rocks within a few feet of cliff dwellings, and most of the specimens collected were sunning themselves on

PLATE 37



View of Navajo Canyon, looking north. The edges of mesas are rimmed by sandstone bedrock, and pinyon-juniper woodland occurs on talus slopes and tops of mesas. The bottom of the canyon, here, is approximately 700 feet below the mesa top.

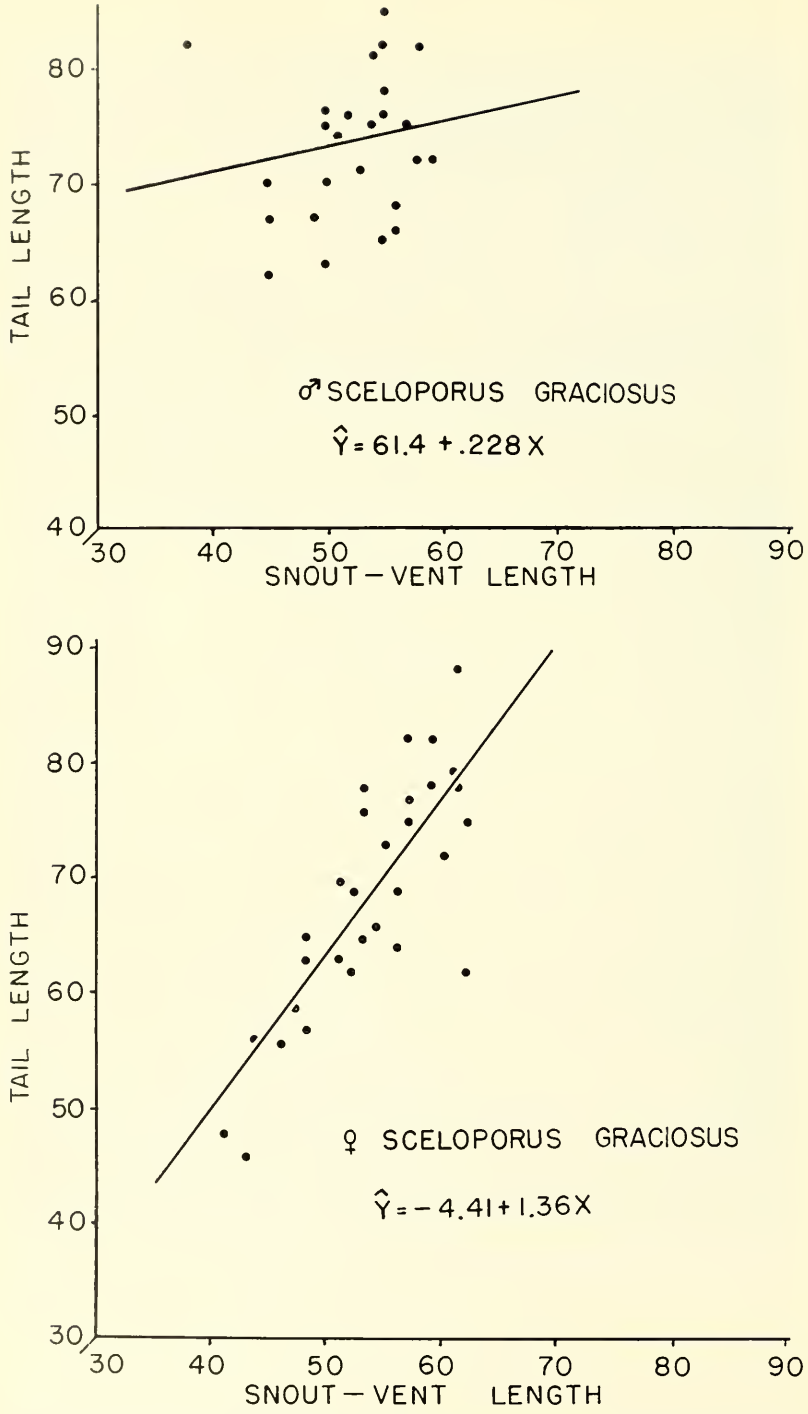


Fig. 4. Scatter diagram of length of body (snout-vent) plotted against length of tail for *S. graciosus*. Measurements are in millimeters; 30 females, 26 males. Regression line is fitted to data by method of least squares.

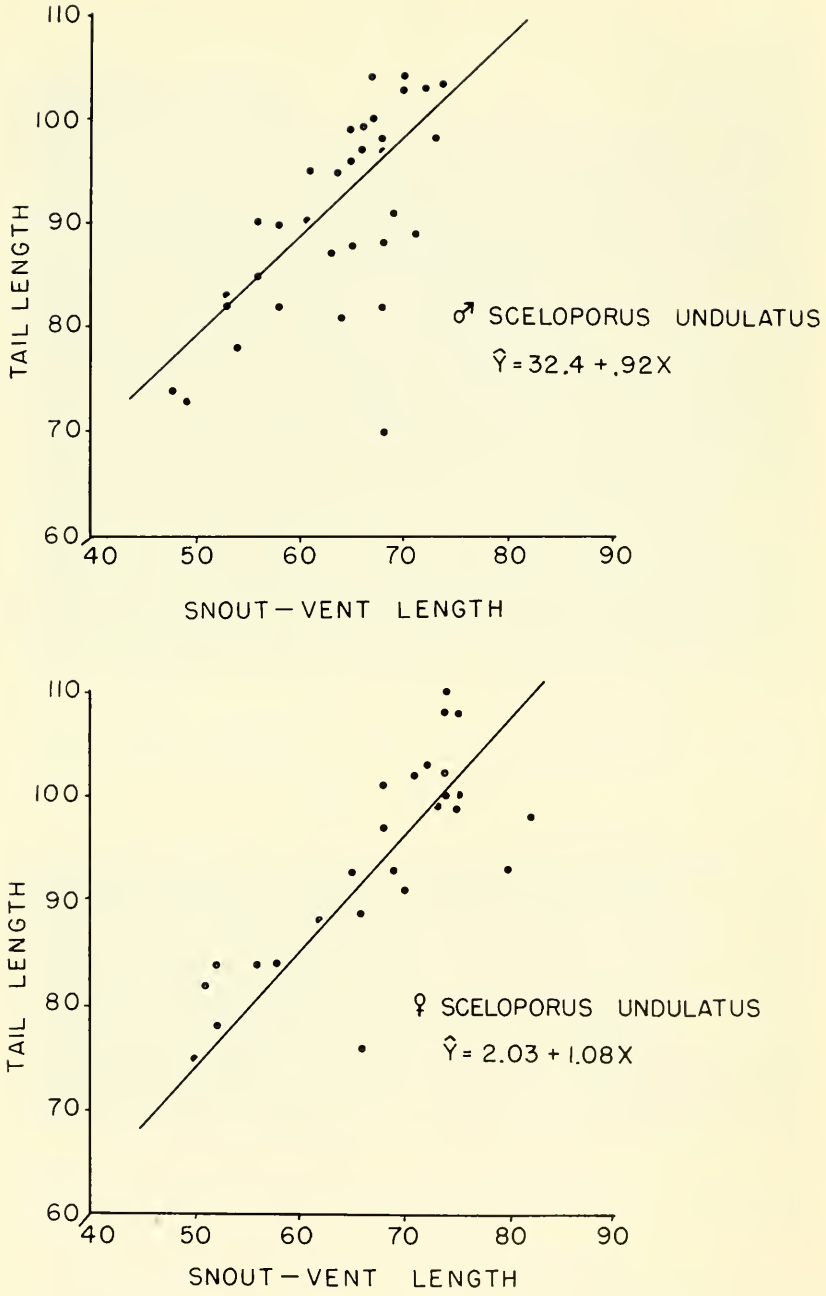


FIG. 5. Scatter diagram of length of body (snout-vent) plotted against length of tail for *S. undulatus*. Measurements are in millimeters; number of females is 30 and number of males, 35. Regression line is fitted to data by method of least squares.

FIG. 1. View of a small portion of the Morfield Burn, showing dense growths of grasses, *Bromus inermus*, *B. japonicus*, and *Agropyron smithii*, that were seeded in 1939 after fire destroyed more than 2000 acres of woodland in the eastern portion of the park. Indian ricegrass, *Oryzopsis hymenoides*, an early invader of denuded areas is also present. The dead trees are mostly pinyon pine and Utah juniper.

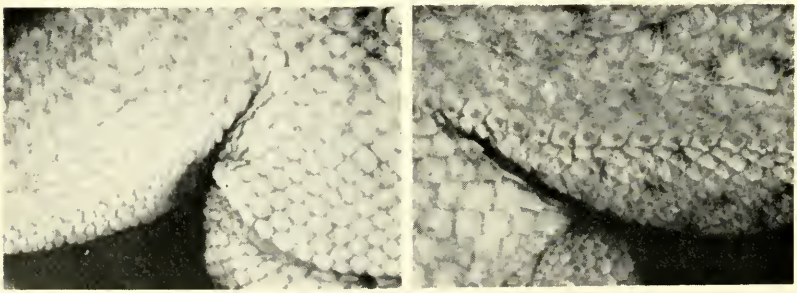


FIG. 2. Ventral views of thigh of female lizards, showing vestigial femoral pores in *Sceloporus graciosus* (left), KU 80652, Sage Flat, S. Chapin Mesa, 1 July 1963, and larger pores in *S. undulatus* (right), KU 80655, Cliffs above Swallow's Nest, 20 June 1963. Femoral pores are more pronounced in males of both species. × 4.

boulders. Only one lizard was taken while descending from a tree. Some escaped capture by running over the edge of a cliff and walking, or running, head-first, down the vertical face of rock. Mittleman (1942:147) notes that members of this species avoid a horizontal position; this was so in Mesa Verde.

Six gravid females contained from three to five ova each, with an average of four. The ova were generally larger (about 7 by 12 mm.) in specimens collected in late June and early July than in other months. Eggs were small in females collected on 20 May and 5 June 1964, measuring 2.6 by 2.6 and 4 by 4 millimeters, respectively. Some females evidently breed early in spring, for a specimen collected on 15 May 1964 contained three eggs measuring 6.8 by 11.8 mm. Young of the year were first seen on 28 August 1963 just outside the park on the southern end of Moccasin Mesa. On that date the snout-vent lengths of two young lizards measured 24 and 25 millimeters.

Many aphids were in stomachs of several lizards, indicating that they climbed into nearby vegetation in order to feed. Ground cover in the collecting area was sparse; hence the aphids probably came from leaves on brush or trees in the area. *Cercocarpus montanus, Amelanchier utahensis, Fendlera rupicola, Pinus edulis,* and *Juniperus osteosperma* were the common woody plants present. Other food items identified in the stomachs of eleven *Urosaurus* were the following arthropods:

Thysanoptera (thrips)
Coreidae (squash bugs)
Tingidae (lace bugs)
Lygaeidae (lygus bugs)
Anthocoridae (Flower bugs)
Aphidae (aphids)
Psyllidae (jumping plant lice)
Cicadellidae (leafhoppers)
Fulgoridae (plant hoppers)
Tenebrionidae (darkling beetles)
Staphylinidae (rove beetles)
Chrysomelidae (leafhopper beetles)
Phyllophaga (June beetles)
Haliplidae (crawling water beetles)
Pselaphidae (ant-loving beetles)
Anthicidae (ant-like flower beetles)
Miridae (plant bugs, including *Halictus* sp.)
Trichoptera (caddis flies)
Lepidoptera (butterflies, moths)
Geometridae (measuring worms)
Orthorrhapha (straight seamed flies)
Rhagionidae (snipe flies)
Chalcidae (chalcid flies)
Bombyliidae (bee flies)
Cecidomyidae (gall midges)
Clistogastra (wasps)
Muscidae (houseflies)
Cynipidae (gall wasps)
Therevidae (stiletto flies)
Bibionidae (March flies)
Otitidae (picture wing flies)
Sarcophagidae (flesh flies)
Scelionidae (scelionids)
Braconidae (braconids)
Formicidae (ants)
Campanotus vicinus
Lasius niger neoniger
Crematogaster lineolata
Acarina (mites)
Erythraeidae
Araneida (spiders)
Lycosidae
Chloropidae (frit flies)
Noctuidae (noctuid moth, larvae)
Ichneumonidae (ichneumon flies)
Chrysopidae (lace wing larvae)

Urosaurus ornatus is parasitized by the nematode *Pharyngodon giganticus,* a common parasite of most lizards within Mesa Verde.

Uta stansburiana stansburiana Baird and Girard

Northern Side-blotched Lizard

Specimens examined.—Total 9: S. Chapin Mesa, USNM 88613.

Additional Records.—Mesa Verde National Park, BYU 2920.

Some specimens examined from outside the National Park.—Drainage 100 yds. W of gravel pit, S. Chapin Mesa, 486, 763; Soda Tip-Off Trail, S. Chapin Mesa, 517-518, 617-618, 749-750.

The side-blotched lizard is restricted in distribution more than any other iguanid within the park. I found this species locally abundant in only two places, both of which were just outside the park along rocky cliffs on the southern rim of Chapin Mesa. Individuals were also seen inside the park in several other places along the edges of Chapin Mesa where outcroppings of sandstone form a bedrock rim.

In all observed cases, *Uta stansburiana* occurs in the same habitat, and in conjunction with, *Urosaurus ornatus;* the converse is not true. The food niches of these two lizards appear to differ enough to permit their coexistence within the same area (see Knowlton, 1943, 1946). The coloration of utas, collected while sunning on boulders or sandstone outcroppings, closely approximated that of the sandstone upon which they were found. No other lizard in the park so closely approaches the color of its habitat.

Of gravid females collected on 15 and 20 May 1964 one contained two small ova (4 by 5 mm.) and each of the other two contained four larger ova (about 6 by 11 mm.). Stebbins (1954: 253) reports that eggs ready for laying measured approximately six to eight by 10 to 12 millimeters and were found in females from April to early July. Smith (1946:280) reports that three or four eggs are laid in early July, or possibly late June, and hatch between late July and mid-August. The large ova in the specimens mentioned above indicate a laying date in early June, but the data are unfortunately meager.

Young of the year were observed for all lizards except *Uta stansburiana* and *Crotaphytus.* This is not surprising, for *Uta* is relatively scarce within Mesa Verde; only eight specimens were taken in three summers of collecting.

Uta stansburiana is parasitized by the nematode *Pharyngodon giganticus.*

Phrynosoma douglassi ornatissimum Girard

Mountain Short-horned Lizard

Specimens examined.—Total 4: Loop Road, ⅛ mi. E Park Headquarters, 6975 ft., Chapin Mesa, 435; Station 6, 4 mi. S of North Rim, Moccasin Mesa, 7525 ft., 527; Morfield-Prater divide, 8000 ft., MVNP; North Rim above Prater Canyon, MVNP.

Additional Records.—Mesa Verde National Park, CU 7458; Prater Canyon, 7600 ft., CU 5591.

The horned lizard is found in diverse types of vegetation, and in all areas of the park. Most of the localities of capture mentioned above are in pinyon-juniper woodland. One lizard was seen in the summer of 1962 in the area of the Morfield Burn. Individuals have been seen in grassy areas, near oak thickets, on the north rim of the park at elevations of about 8300 feet.

Young lizards, less than one inch in total length, were first seen on 5 August 1963 on Moccasin Mesa. Other young individuals of about the same size were seen in different locations on 6, 14, 21 and 30 August 1963.

The food of this lizard consists primarily of arthropods; it is known to feed upon ants, grasshoppers, beetles, larval moths, caterpillars and butterflies (Smith, 1946:306; Stebbins, 1954:260). The stomach of an individual found dead on a park road contained scores of ants.

Because of its slow movement, its habit of running only short distances, and its bizarre appearance, horned lizards are often caught by visitors and removed from the park. This is deplorable and contrary to Park policy.

Cnemidophorus velox Springer

Plateau Whiptail Lizard

Specimens examined.—Total 16: Spruce Canyon, 506; Rocks above Mug House, Wetherill Mesa, 591; Wetherill Mesa Lab, 7200 ft., Chapin Mesa, 820; Sun Tower, CU 4345-4348; Main Camp, CU 18643; Soda Canyon, 6000 ft., MVNP; Spruce Tree Canyon, MVNP; Mesa Verde National Park, USNM 88603.

Additional Records.—Mesa Verde National Park, AMNH 13606-13607.

Some specimens examined from outside the National Park.—Southern tip Chapin Mesa, 6500 ft., 392, CU 4349-4352.

These lizards were found mostly at lower elevations along the southern halves of the mesas, and appear to be locally abundant

around Park Headquarters. They were seen frequently in Spruce Canyon and Spruce Tree Canyon, but were not seen so often as other lizards when I made a weekly trip, throughout the year, through these canyons into Navajo Canyon, in order to service weather stations. These lizards are more secretive than *Scleroporus*, and thus could be more abundant than they appear to be.

Gravid females were collected on 23 June 1963 and 10 June 1964, and contained three to five ova (9 by 7 and 8 by 10 mm.), respectively. Young of the year were first seen on 30 August 1963 on Moccasin Mesa just outside the park. One young measured 33 mm. snout-vent length and 66 mm. tail length.

When fed ants, a captive darted about her cage catching them almost as rapidly as they were introduced; mealworms were eaten with less speed, perhaps due to their sluggish movement. When eating earthworms or mealworms, the lizard took the worm in her mouth and shook it vigorously, striking the worm against the sand in the bottom of the cage, and often breaking it in half. The half in the mouth was chewed rapidly and swallowed, then the other half was eaten.

A captive showed a strong tendency to dig under things; the small water-container in its cage was customarily overturned by efforts to dig under it. When this happened, the lizard would begin a new tunnel. Under natural conditions these lizards probably dig hibernacula under rocks, thereby obtaining added protection against precipitation that could cause collapse of their tunnels.

When digging the hibernaculum, the captive began a hole by throwing sand rearward with powerful strokes of the front feet. The lizard then thrust its head in the opening and continued to dig downward until the tunnel was deep enough to accommodate most of its body. At this point the front feet pushed sand backward and the hind feet moved it out of the tunnel. The lizard then excavated a cavity at the bottom of the tunnel and turned completely around in it. Sand was now pushed anteriorly and laterally by means of the front feet. The lizard then left the tunnel and began a second tunnel leading into the chamber. When the second entrance was complete, the animal retreated to the chamber and closed the outer openings of both entrances with sand. The resulting chamber was three inches below the surface of the sand, the depth being limited by the bottom of the cage. Each tunnel entered the chamber at an angle of about 45 degrees. It was observed through the glass bottom of the cage that the chamber was

barely large enough for the lizard to lie in and turn around in, when the body and tail were bent into a U shape.

The whip-tailed lizards of the park are parasitized by cestodes, *Oochoristica bivitellolobata* Loewen; nematodes, *Pharyngodon gi-ganticus;* and trematodes, *Phyllodistomum* sp.

Eumeces multivirgatus gaigeae Taylor

Two-lined Skink

Specimen examined.—Total 1: Morfield Canyon, 7500 ft., in oak brush 1500 ft. SE of Morfield Well, 374.

Only the one individual was found. It was obtained on 20 June 1963 at the edge of an oak thicket on the east side of Morfield Canyon, at the base of the second drainage south of the well. The skink scurried under oak leaves as I approached, but I managed to shoot it. This specimen is the first *Eumeces* to be reported from Montezuma County, although *E. m. gaigeae* has been found in La Plata County, which adjoins Montezuma County on the east (Smith and Maslin, 1965).

Thamnophis elegans vagrans (Baird and Girard)

Wandering Garter Snake

Specimens examined.—Total 3: ¼ mi. S Far View Ruins, 7500 ft., Chapin Mesa, 470; Wetherill Mesa Road, 2 mi. E of Wetherill Mesa's north rim, 336; ½ mi. S Far View Ruins, 7575 ft., Chapin Mesa, 472.

Additional Record.—Mesa Verde National Park, MVZ 40772-40773.

The garter snakes of the park are all of one species, *Thamnophis elegans,* the most nearly ubiquitous snake in Colorado. The above-mentioned localities are from the middle of the park and its northern end. These snakes were usually seen in the shaded, lower branches of bushes. Only one garter snake was seen moving about in open pinyon-juniper woodland; it had apparently been sunning until I startled it. Garter snakes were seen also at Park Point and in the Montezuma Valley immediately north of the park's boundary. A young individual, CU 25674, was obtained from Chicken Creek, in the La Plata Mountains, where the snake had submerged to escape from me.

Captives that had not fed for more than two weeks ate adult scelopori. Small individuals of *Bufo punctatus* were eaten, but mice were not eaten. The captives spent most of their time curled up in their water dishes and were frequently observed to drink. In the San Juan Basin of New Mexico, Harris (1963:25) found garter

snakes in or near thick vegetation and noted that they seemed not to require free water. This also appears to be the situation in Mesa Verde; the snakes live in the higher, cooler parts of the park, usually in heavy vegetation. Water loss would be minimized in this habitat, and metabolic water likely provides sufficient moisture to sustain them between rains. It is also unlikely that they could survive between rains without relying heavily upon metabolic water.

Specimens from the park vary in the intensity of ground color, color of the markings, and to a lesser degree in shape of markings. Juveniles are paler than adults; the ground color is tan in juveniles rather than some combination of brown.

Masticophis taeniatus taeniatus (Hallowell)

Desert Striped Whip Snake

Specimens examined.—Total 7: Utility Area, 7090 ft., Chapin Mesa, 197; 100 yds. S Entrance Station, 631; ¼ mi. S Far View Ruins road, 7625 ft., Chapin Mesa, 672; 0.6 mi. N Far View Group (by road), Chapin Mesa, 766; Navajo Hill, 8100 ft., Chapin Mesa, 788; near Park Museum, MVNP; Mesa Verde National Park, MVNP.

Striped whipsnakes are found on top of the mesas, and may be seen in Spruce Tree Canyon. The specimens that I collected were found dead on the park road in the vicinity of Navajo Hill southward to Park Headquarters. In the 28 months I spent in the park, more snakes of this species seem to have been hit on the road in this area than elsewhere. The seeming concentration from Park Headquarters to Navajo Hill may be an artifact due to the large number of automobiles traveling in this area. Snakes cannot get adequate traction on road surfaces, and therefore are the more vulnerable to traffic. Nevertheless, I did not see this species on the southern ends (perhaps the southern quarters) of the mesas, and do not know of any that were killed on the loop road (southern Chapin Mesa) while I was in the park.

In Mesa Verde these snakes appear to be associated with pinyon-juniper woodland, or moist secondary canyons such as Spruce Tree Canyon.

Maslin (1959:59) lists the range of this subspecies as extreme western Colorado below 7000 feet, and Stebbins (1954:379) states that the California subspecies reaches elevations of at least 6300 feet. *Masticophis t. taeniatus* has a range of distribution in the park from about 7000 to at least 8100 feet.

Stomachs of three of the above-mentioned specimens contained an adult *Sceloporus graciosus,* one young *Phrynosoma douglassi,* and fur of *Peromyscus* sp.

Opheodrys vernalis blanchardi Grobman

Western Smooth Green Snake

Specimens examined.—Total 2: Navajo Hill, MVNP; Mesa Verde National Park, MVNP.

The first smooth green snake found in Mesa Verde was obtained in 1930 by Mr. Paul R. Frank, then Ranger-Naturalist. This snake was found near Far View House, and another was reported to have been seen in the same locality (Barry, 1933). The above-mentioned specimen has evidently been lost, for I find no trace of it; the two specimens in the park's collection were taken in 1952 and 1948.

My wife and I saw, but were unable to catch, an *Opheodrys* at Park Point on 6 August 1962. This species is not abundant within the park.

Pituophis melanoleucus deserticola Stejneger

Great Basin Gopher Snake

Specimens examined.—Total 11: Wetherill Road, 1.1 mi. W of Chapin gate, 7900 ft., 601; ¼ mi. S Far View Ruins road, 7625 ft., Chapin Mesa, 672; Log Cabin, Campground No. 1, 7000 ft., Chapin Mesa, 692; Wetherill Mesa, 3.5 mi. S of North Rim, 7850 ft., 263; Cliff Palace Road, 1 mi. ENE Park Headquarters, 6975 ft., 574; 1 mi. SE Montezuma Overlook (by road), 803; Park Road, 2 mi. NE Park Headquarters, 806; Park Headquarters, MVNP; Mesa Verde National Park, MVNP, KU 51490.

Additional Records.—Sun Tower Ruins, CU 4903.

Some specimens examined from outside the National Park.—Southern end Chapin Mesa, 399.

Gopher snakes are probably the most common snake of Mesa Verde; they are found at all elevations and seem to prefer wooded areas. They are attracted to the warmth of the park road during evening and early morning hours, and unfortunately the mortality of this beneficial snake is high, for the park road is heavily traveled.

Individuals of *Pituophis* on Mesa Verde vary in the amount of reddish brown coloration in the dorsal blotches. Some specimens have pronounced black dorsal blotches throughout their length, whereas others have brownish patterns on the mid-body. The anterior blotches tend to coalesce with each other and with the first lateral series of blotches. Some brownish scales are within the black, dorsal blotches of all specimens, and all individuals have definitely black blotches anteriorly and caudally. The above, and other characters, fit the description for *P. m. deserticola* (Klauber, 1947). Young individuals have brownish blotches wherein the scales tend to be rimmed with black pigment, which encroaches upon the rest of the scale with maturation.

The specimens I examined have one preorbital, or two; the typical three distinct lines on the head; four prefrontals, and a slightly elevated rostral scale that is either as long as, or slightly longer than, it is wide.

Intergradation between *P. m. affinis* and *P. m. deserticola* has recently been reported for northwestern New Mexico (Gehlbach, 1965:309). This zone of intergradation does not include Mesa Verde, and the gopher snakes of the park are of the subspecies *deserticola.*

Captives were fed mice and chipmunks. When two or more snakes were in one cage one snake would kill the prey and start to swallow it; then another snake would often try to swallow the opposite end of the prey. This would result in a tug of war with much writhing and hissing by the contestants. The winner was usually that one that had originally caught the mouse or chipmunk. Snakes with eyes clouded preparatory to shedding would hiss and strike at mice or chipmunks, but usually missed them; the animals were eaten if caught, however. Captives ate adult sceloporı when sufficiently hungry. One large *Pituophis* (about four feet long) regurgitated a juvenal white-throated wood rat, when captured.

In order to prove to myself and coworkers that gopher snakes and rattlesnakes are compatible. I placed an individual of each species in a six foot square cage. The snakes ignored each other. Neither attempted to harm the other and the rattlesnake frequently crawled across the outstretched gopher snake, and vice versa. After an especially cool night they were found curled up in the same nesting box, which measured 11 by 11 by 11 inches. Other captives behaved in an identical manner. This does not, of course, indicate other possible interactions or relationships between the two species in nature. Gopher snakes and rattlesnakes have been observed to issue from hibernation from the same den in South Dakota (Klauber, 1947:53).

Preliminary results of a food study indicate that scats of *Pituophis* contain, by weight, an average of 50 per cent moisture. Some free water is also lost upon defecation and has not yet been adequately measured. The captives concerned had periodic access to water, but considering how infrequently they were observed to drink, it appears that most of the water represented in the scats was derived metabolically. An analysis of this and other feeding experiments will be presented elsewhere.

Lampropeltis doliata celaenops Stejneger

New Mexico Milk Snake

Specimens examined.—Total 2: Spruce Tree Lodge, MVNP.

Some specimens examined from outside the National Park.—Near Cortez, Colorado, MVNP.

The above is the only specimen of this species that has been found in the park. There is a second specimen in the park's collection that was taken "near Cortez," Colorado. A milk snake was seen in the summer of 1964 under a rock at Sun Temple, and escaped down a hole.

Tanner and Loomis (1957:31) consider the specimen from Mesa Verde to be an intergrade between *celaenops* and *taylori.*

Hypsiglena torquata loreala Tanner

Mesa Verde Night Snake

Specimens examined.—Total 5: 100 yds. N Spruce Tree Ruin, by trail, 721; Chapin Mesa, CU 5801, 11678; Sun Temple, 6800 ft., MVNP; 1 mi. N Far View Ruins, 7900 ft., MVNP.

Additional Record.—Sun Temple, BYU 2.

Specimens from Mesa Verde were cited in the original description of this subspecies (Tanner, 1944:63), and the first Colorado record was of specimens from Mesa Verde (Barry, 1932). This small, secretive snake may be present in larger numbers than would be estimated from the number of specimens in museum collections. My specimen was picked up by Mr. A. Hewitt, Assistant Chief of Interpretation, on the trail to Spruce Tree Ruin, where someone had stepped on it.

Crotalus viridis subsp.?

Rattlesnake

Specimens examined.—Total 14: Entrance to Wetherill Road, 5½ mi. N Park Headquarters, Chapin Mesa, 7936 ft., 462; 2 mi. N Rock Springs, 8000 ft., Wetherill Mesa, 468; Pictograph Point Trail, 6900 ft., Chapin Mesa, 564; Wetherill Mesa Road, Head E. Fork Navajo Canyon, 8175 ft., 633; North end Wetherill Mesa, 691; Park Point, 805, 798, 819; Mesa Verde National Park, 7500 ft., CU 7494; 100 yds. N Spruce Tree Ruin, MVNP; Morfield, MVNP; Mesa Verde National Park, MVNP; 2 mi. NNW Rock Springs, KU 51515.

Additional Records.—Mesa Verde National Park, BYU 21266.

Mesa Verde is in an area where intergradation has been thought to occur between the three subspecies *C. v. viridis, C. v. concolor,* and *C. v. nuntius* (L. M. Klauber, personal communication).

The rattlers in the park are seen more often at higher elevations

(8000 ft. and above) than elsewhere, although individuals are occasionally found in canyons. Figure 6 shows the localities where rattlesnakes were observed, obtained, or killed from 1959 through 1964.

The largest specimen is 33.5 inches long and is a fairly typical *C. v. viridis*. The remaining individuals are about 24 inches long but are not typical of either *nuntius* or *concolor*.

Six of my specimens were inspected by L. M. Klauber, who determined that on the basis of size and development of rattle strings, they appear to be stunted offshoots of *C. v. viridis*. When I first examined those and additional specimens, I considered them to be *C. v. nuntius*, which would be in agreement with the findings of McCoy (1962). Klauber thinks that in color and markings the six snakes are more nearly like *concolor* than *nuntius*. In view of their size, their propensity for higher elevations, and their coloration, the rattlesnakes of Mesa Verde are here considered as intergrades between *C. v. viridis* and *C. v. concolor*.

This rattlesnake is generally docile and retreating, preferring to escape rather than to stand its ground. The specimens that I caught did not rattle until lifted off the ground by means of a tong type snake stick. When placed on the ground for photographing, the snakes moved away and it was necessary to pick them up repeatedly and replace them in the desired spot. In spite of this harassment, none of the snakes coiled, but merely elevated the tail and rattled vehemently while crawling away. Repeated captures caused them to bite the snake stick, but they did not attempt to strike at several people standing nearby.

Rattlesnakes formerly were killed on sight by rangers, tourists and members of the maintenance staff. The nearly universal dislike for rattlers is understandable. Today's National Park policy properly prohibits killing them; the national parks and monuments in a few years will be about the only refugia left in which these snakes can survive. The killing of rattlesnakes in national parks and monuments adversely affects the ecology of the area concerned. Rattlesnakes and other snakes are certainly more beneficial than harmful in helping to prevent overpopulation of prey species. Snakes occurring in the areas heavily used by visitors should be removed and released elsewhere.

Few park visitors recognize a rattlesnake when they see one. The illustrated brochure given to each visitor at the entrance station might well contain a photograph of a Mesa Verde rattlesnake and a few words of description and caution.

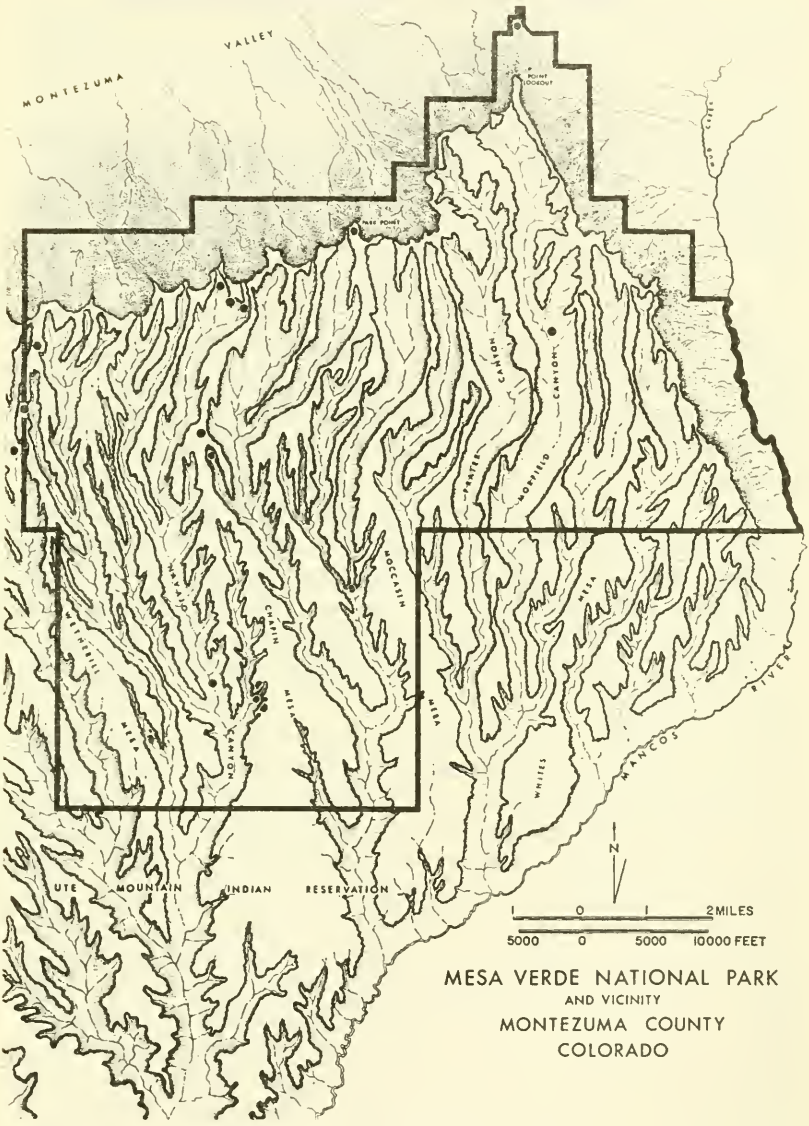


FIG. 6. Map of Mesa Verde National Park and vicinity. Dots indicate localities where rattlesnakes were killed, collected, or observed in the period 1961-1964.

A SPECIES OF UNVERIFIED OCCURRENCE

Scaphiophus hammondi Baird

Hammond's Spadefoot Toad

In the collection of the University of Colorado there are thirty specimens of this toad taken from McElmo Creek, 5 mi. W Cortez, Montezuma County, three miles west of the park. Spadefoot toads probably occur also along the Mancos River.

DISCUSSION

The fauna of Mesa Verde is predominately Upper Sonoran in affinity. Boreal mammals are present, but are restricted to the higher, cooler parts of the park (Anderson, 1961:65). Some Boreal species, such as the dusky grouse, are found only along the northern escarpment.

Snakes appear to prefer the higher parts of the park, from about 7000 to 8500 feet. *Crotalus viridis* especially is more common at the higher elevations, indicating its affinity with the more northern subspecies *concolor*, rather than the more southern subspecies *nuntius*. *Pituophis* and the scelopori are more nearly ubiquitous in distribution, ranging from high to low elevations wherever the habitat is suitable.

Species restricted to lower elevations include *Uta stansburiana, Eumeces multivirgatus, Ambystoma tigrinum, Rana pipiens, Bufo punctatus* and *Bufo woodhousei*. The amphibians are dependent upon a ready supply of water. *B. woodhousei* apparently meets its needs by inhabiting areas near the wells in Prater Canyon. *Bufo punctatus* ranges farther from permanent water and seems to inhabit bedrock drainages where pot holes contain enough water in mid-summer and autumn in which to lay eggs. Many of these eggs hatch and reach maturity, but many more are lost when water evaporates from the pools, or when heavy rains wash the eggs or tadpoles out of the pot holes and onto dry bedrock. Both species of *Bufo* may inhabit springs and seeps within the park, but were not observed to be present in those places. Both species of *Bufo* are likely to be found also in riparian habitats along the Mancos River. Only *Rana pipiens* is restricted to the riparian habitat.

Each species of lizard is geographically sympatric with at least one other species within the park. Areas of sympatry occur at the peripheries of ranges. *Sceloporus undulatus* and S. *graciosus* are sympatric where boulders, bedrock drainages, or sandstone

outcrops adjoin pinyon-juniper woodland. Both are found in brushy areas on rocky slopes where brush is ecotonal between pinyon-juniper woodland and bedrock, or between woodland and sagebrush. The preferred habitat of *S. graciosus* is pinyon-juniper woodland where shade and cooler temperatures prevail; *S. undulatus* prefers a habitat in which there are boulders or exposed bedrock.

Some individuals of *S. undulatus* live along rocky talus slopes or cliffs in company with *Urosaurus ornatus, Uta stansburiana* and *Crotaphytus.* All of these lizards are found in rocky areas. *Uta* and *Urosaurus* are common along cliffs where these is exposed bedrock and vertical faces. These areas generally have scattered pinyons and junipers or ponderosa pine; the vegetation adjacent to cliffs usually consists of brush (*Cerococarpus, Amelanchier, Fendlera*), or a pinyon-juniper woodland with a heavy brush understory. Such exposed bedrock areas rim the edges of the mesas. In some places the forest grows to within a few feet of the edge, leaving only several feet of bedrock exposed, but in other places the bedrock extends fifty feet or more from the edge of the woodland before terminating in a cliff. In most places the amount of rock exposed along the rims of the mesas is between one and 50 feet, probably averaging about 10 feet.

Crotaphytus and *Scleroporus undulatus,* as already stated, live on these exposed areas of rock. Broken boulders and great vertical cracks in the bedrock may allow retreat from the sun or from predators. *Sceloporus graciosus* may venture onto such areas, but generally stays within a few feet of vegetation abutting upon exposed bedrock. *Uta* and *Urosaurus* are found near the edges of precipitous cliffs and most escape routes are down the faces of cliffs.

Sceloporus undulatus and *S. graciosus* are geographically sympatric with *Crotaphytus* and *Cnemidophorus* in canyons. Both *Cnemidophorus* and *S. graciosus* are found in brush along slopes, or in sagebrush and grassy areas toward the bottom of the canyon; they usually stay close to heavy cover. *S. undulatus* inhabits boulders in the bottoms of canyons, or on talus slopes. *Crotaphytus* lives both in the bottoms of canyons and along talus slopes where its prey lives.

Phrynosoma is found in pinyon-juniper woodland, grassy areas, and in brushy ecotonal areas. Within these habitats it is geographically sympatric with *S. graciosus. Phrynosoma* is more tolerant of high temperatures, and is often seen in unshaded places during the hottest parts of the day.

Several species of lizards occupy the same areas within Mesa Verde, where their ranges overlap. Although the lizards are sympatric in these areas in a geographical sense, they appear to be ecologically allopatric.

The nematode *Pharyngodon giganticus* occurs in most, if not all, of the Mesa Verde lizards. This parasite is here recorded for *Sceloporus undulatus, S. graciosus, Urosaurus ornatus, Uta stansburiana, Crotaphytus collaris,* and *Cnemidophorus velox.* This indicates that all of the lizards eat the same arthropods containing the parasite, or that the parasite has a wide range of intermediate hosts among the arthropods of the park. *Crotaphytus* may be infected by eating infected lizards, rather than arthropods.

Hibernation of lizards in the park is apparently triggered by lower temperatures resulting from the decreased angle of insolation during September and October. Insects are abundant for several weeks after all lizards have gone into hibernation, indicating that food shortage is probably not a factor. As daylight hours grow shorter, and the sun's rays are intercepted more and more by the canyon walls, the talus slopes and canyon bottoms are heated appreciably less during the day. Since these animals rely directly or indirectly upon insolation for warmth and its resultant activating influence, they appear to be dependent upon some minimal amount of insolation for normal activity. Lizards may hibernate when insolation falls below this minimum, and they cannot obtain enough warmth from the substrate. The time of hibernation is not the same for all adults, and this is perhaps due to how their habitat receives the sun. Lizards on different facing slopes would thus be expected to hibernate at different times.

I suspect this rationale might explain why *Cnemidophorus,* an inhabitant of cool canyons, is not seen until a week or two after *Sceloporus* emerges from hibernation. Narrow canyons such as Spruce Tree Canyon are not warmed by insolation so early in spring as are the tops of mesas or talus slopes in wider canyons. Higher temperatures may also be required for activating *Cnemidophorus* than for activating *Sceloporus.*

Emergence from hibernation in spring appears to be linked with increased warming of the soil with a resultant drying of the surface.

LITERATURE CITED

ANDERSON, S.
1961. Mammals of Mesa Verde National Park, Colorado. Univ. Kansas Publ. Mus. Nat. Hist., 14:29-67, 2 pls., 3 figs.

BARRY, L. T.
1932. An extension of the range of four reptiles to include Colorado. Copeia, 1932 No. 2: 103.
1933. Notes on Colorado reptiles. Copeia, 1933 No. 2:99-100.

CARY, M.
1911. A biological survey of Colorado. N. Amer. Fauna, 33:1-256, 12 pls., 39 figs.

DICE, L. R.
1962. Natural communities. Univ. of Michigan Press, Ann Arbor, pp. v-x, + 1-547, 52 figs. in text.

FITCH, H. S., and TANNER, W. W.
1951. Remarks concerning the systematics of the collared lizard, Crotaphytus collaris with a description of a new subspecies. Trans. Kansas Acad. Sci., 54:548-599, 2 figs.

GEHLBACH, F. R.
1965. Herpetology of the Zuni Mountains Region, northwestern New Mexico. Proc. U. S. Nat. Mus., 116:243-332, 4 pls., 10 figs.

HARRIS, A. H.
1963. Ecological distribution of some vertebrates in the San Juan Basin, New Mexico. Mus. New Mexico Papers in Anthro. No. 8:7-64, 11 figs. in text.

KLAUBER, L. M.
1947. Classification and ranges of the gopher snakes of the genus Pituophis in the western United States. Bull. Zool. Soc. San Diego, No. 22:7-81, 6 figs.

KNOWLTON, G. F.
1942. Range lizards as insect predators. Jour. Econ. Entomol., 35(4): 602.

KNOWLTON, G. F., FRONK, W. D., and MADDOCK, D. R.
1943. Seasonal insect food of the brown-shouldered Uta (Lizard). Jour. Econ. Entomol., 35(6):942.

KNOWLTON, G. F., MADDOCK, D. R., and WOOD, S. L.
1946. Insect food of the sagebrush swift. Jour. Econ. Entomol., 39(3): 382-383.

KNOWLTON, G. F., and NYE, W. P.
1946. Lizards feeding on ants in Utah. Jour. Econ. Entomol., 39(4):546.

KNOWLTON, G. F.
1947. The sagebrush swift in pasture insect control. Herpetologica, 4:25.
1948. Ladybird beetles in sagebrush swift stomachs. Herpetologica, 4:151.
1948. Vertebrate animals feeding on the mormon cricket. Amer. Midl. Nat., 39:137-138.
1953. Some insect food of Sceloporus g. graciosus. Herpetologica, 9:70.

KNOWLTON, G. F., and BALDWIN, B. A.
1953. Ants in horned toad. Herpetologica, 9:70.

MASLIN, T. P.
1959. An annotated check list of the amphibians and reptiles of Colorado. Univ. Colorado Studies, Series in Biology, No. 6, Univ. Colorado Press, Boulder, pp. i-vi + 1-98.
1964. A check list of the amphibians and reptiles of Colorado, revised by Hobart M. Smith, mimeo. 5pp.

MCCOY, C. J., JR.
1962. Noteworthy amphibians and reptiles from Colorado. Herpetologica, 18:60-62.

MITTLEMAN, M. B.
1942. A summary of the iguanid genus Urosaurus. Bull. Mus. Comp. Zool., Harvard, 91:106-181, 16 pls., 9 figs.

SMITH, H. M.
1946. Handbook of lizards. Comstock Publishing Co., New York, pp. vii-xxi, + 1-557, 135 pls., 136 figs., 41 maps.

SMITH, H. M., MASLIN, T. P., and BROWN, R. L.
1965. Summary of the distribution of the herpetofauna of Colorado. Univ. Colorado Studies, Series in Biol., No. 15:1-52.

STEBBINS, R. C.
1954. Amphibians and reptiles of western North America. McGraw-Hill, New York, pp. vii-xxii + 1-536, 104 pls., 52 figs.

TANNER, W. W.
1944. A taxonomic study of the genus Hypsiglena. Great Basin Nat., 5(3&4):25-92, 4 pls.

TANNER, W. W., and LOOMIS, R. B.
1957. A taxonomic and distributional study of the western subspecies of the milk snake, Lampropeltis doliata. Trans. Kansas Acad. Sci., 60:12-42, 4 pls.

Transmitted July 26, 1965.

30-8424

30-3966

(Continued from inside of front cover)

Vol. 13. 1. Five natural hybrid combinations in minnows (Cyprinidae). By Frank B. Cross and W. L. Minckley. Pp. 1-18. June 1, 1960.
2. A distributional study of the amphibians of the Isthmus of Tehuantepec, México. By William E. Duellman. Pp. 19-72, pls. 1-8, 3 figures in text. August 16, 1960. 50 cents.
3. A new subspecies of the slider turtle (Pseudemys scripta) from Coahuila, México. By John M. Legler. Pp. 73-84, pls. 9-12, 3 figures in text. August 16, 1960.
*4. Autecology of the copperhead. By Henry S. Fitch. Pp. 85-288, pls. 13-20, 26 figures in text. November 30, 1960.
5. Occurrence of the garter snake, Thamnophis sirtalis, in the Great Plains and Rocky Mountains. By Henry S. Fitch and T. Paul Maslin. Pp. 289-308, 4 figures in text. February 10, 1961.
6. Fishes of the Wakarusa River in Kansas. By James E. Deacon and Artie L. Metcalf. Pp. 309-322, 1 figure in text. February 10, 1961.
7. Geographic variation in the North American cyprinid fish, Hybopsis gracilis. By Leonard J. Olund and Frank B. Cross. Pp. 323-348, pls. 21-24, 2 figures in text. February 10, 1961.
8. Descriptions of two species of frogs, genus Ptychohyla; studies of American hylid frogs, V. By William E. Duellman. Pp. 349-357, pl. 25, 2 figures in text. April 27, 1961.
9. Fish populations, following a drought, in the Neosho and Marais des Cygnes rivers of Kansas. By James Everett Deacon. Pp. 359-427, pls. 26-30, 3 figures in text. August 11, 1961. 75 cents.
10. North American recent soft-shelled turtles (family Trionychidae). By Robert G. Webb. Pp. 429-611, pls. 31-54, 24 figures in text. February 16, 1962. $2.00.

Index. Pp. 613-624.

Vol. 14. 1. Neotropical bats from western México. By Sydney Anderson. Pp. 1-8. October 24, 1960.
2. Geographic variation in the harvest mouse, Reithrodontomys megalotis, on the central Great Plains and in adjacent regions. By J. Knox Jones, Jr., and B. Mursaloglu. Pp. 9-27, 1 figure in text. July 24, 1961.
3. Mammals of Mesa Verde National Park, Colorado. By Sydney Anderson. Pp. 29-67, pls. 1 and 2, 3 figures in text. July 24, 1961.
4. A new subspecies of the black myotis (bat) from eastern Mexico. By E. Raymond Hall and Ticul Alvarez. Pp. 69-72, 1 figure in text. December 29, 1961.
5. North American yellow bats, "Dasypterus," and a list of the named kinds of the genus Lasiurus Gray. By E. Raymond Hall and J. Knox Jones, Jr. Pp. 73-98, 4 figures in text. December 29, 1961.
6. Natural history of the brush mouse (Peromyscus boylii) in Kansas with description of a new subspecies. By Charles A. Long. Pp. 99-110, 1 figure in text. December 29, 1961.
7. Taxonomic status of some mice of the Peromyscus boylii group in eastern Mexico, with description of a new subspecies. By Ticul Alvarez. Pp. 111-120, 1 figure in text. December 29, 1961.
8. A new subspecies of ground squirrel (Spermophilus spilosoma) from Tamaulipas, Mexico. By Ticul Alvarez. Pp. 121-124. March 7, 1962.
9. Taxonomic status of the free-tailed bat, Tadarida yucatanica Miller. By J. Knox Jones, Jr., and Ticul Alvarez. Pp. 125-133, 1 figure in text. March 7, 1962.
10. A new doglike carnivore, genus Cynarctus, from the Clarendonian Pliocene, of Texas. By E. Raymond Hall and Walter W. Dalquest. Pp. 135-138, 2 figures in text. April 30, 1962.
11. A new subspecies of wood rat (Neotoma) from northeastern Mexico. By Ticul Alvarez. Pp. 139-143. April 30, 1962.
12. Noteworthy mammals from Sinaloa, Mexico. By J. Knox Jones, Jr., Ticul Alvarez, and M. Raymond Lee. Pp. 145-159, 1 figure in text. May 18, 1962.
13. A new bat (Myotis) from Mexico. By E. Raymond Hall. Pp. 161-164, 1 figure in text. May 21, 1962.
*14. The mammals of Veracruz. By E. Raymond Hall and Walter W. Dalquest. Pp. 165-362, 2 figures in text. May 20, 1963. $2.00.
15. The Recent mammals of Tamaulipas, México. By Ticul Alvarez. Pp. 363-473, 5 figures in text. May 20, 1963. $1.00.
16. A new subspecies of the fruit-eating bat, Sturnira ludovici, from western Mexico. By J. Knox Jones, Jr., and Gary L. Phillips. Pp. 475-481, 1 figure in text. March 2, 1964.
17. Records of the fossil mammal Sinclairella, Family Apatemyidae, from the Chadronian and Orellan. By William A. Clemens, Jr. Pp. 483-491, 2 figures in text. March 2, 1964.
18. The mammals of Wyoming. By Charles A. Long. Pp. 493-758, 82 figures in text. July 6, 1965. $3.00.

Index. Pp. 759-784.

(Continued on outside of back cover)

(Continued from inside of back cover)

Vol. 15. 1. The amphibians and reptiles of Michoacán, México. By William E. Duellman. Pp. 1-148, pls. 1-6, 11 figures in text. December 20, 1961. $1.50.
2. Some reptiles and amphibians from Korea. By Robert G. Webb, J. Knox Jones, Jr., and George W. Byers. Pp. 149-173. January 31, 1962.
3. A new species of frog (genus Tomodactylus) from western México. By Robert G. Webb. Pp. 175-181, 1 figure in text. March 7, 1962.
4. Type specimens of amphibians and reptiles in the Museum of Natural History, The University of Kansas. By William E. Duellman and Barbara Berg. Pp. 183-204. October 26, 1962.
5. Amphibians and reptiles of the rainforests of southern El Petén, Guatemala. By William E. Duellman. Pp. 205-249, pls. 7-10, 6 figures in text. October 4, 1963.
6. A revision on snakes of the genus Conophis (Family Colubridae, from Middle America). By John Wellman. Pp. 251-295, 9 figures in text. October 4, 1963.
7. A review of the Middle American tree frogs of the genus Ptychohyla. By William E. Duellman. Pp. 297-349, pls. 11-18, 7 figures in text. October 18, 1963. 50 cents.
8. Natural history of the racer Coluber constrictor. By Henry S. Fitch. Pp. 351-468, pls. 19-22, 20 figures in text. December 30, 1963. $1.00.
9. A review of the frogs of the Hyla bistincta group. By William E. Duellman. Pp. 469-491, 4 figures in text. March 2, 1964.
10. An ecological study of the garter snake, Thamnophis sirtalis. By Henry S. Fitch. Pp. 493-564, pls. 23-25, 14 figures in text. May 17, 1965.
11. Breeding cycle in the ground skink, Lygosoma laterale. By Henry S. Fitch and Harry W. Greene. Pp. 565-575, 3 figures in text. May 17, 1965.
12. Amphibians and reptiles from the Yucatan Peninsula, México. By William E. Duellman. Pp. 577-614, 1 figure in text. June 22, 1965.
13. A new species of turtle, genus Kinosternon, from Central America. By John M. Legler. Pp. 615-625, pls. 26-28, 2 figures in text. June 20, 1965.
14. A biogeographic account of the herpetofauna of Michoacán, México. By William E. Duellman. Pp. 627-709, pls. 29-36, 5 figures in text. December 30, 1965.
15. Amphibians and reptiles of Mesa Verde National Park, Colorado. By Charles L. Douglas. Pp. 711-744, pls. 37, 38, 6 figures in text. March 7, 1966.

More numbers will appear in volume 15.

Vol. 16. 1. Distribution and taxonomy of mammals of Nebraska. By J. Knox Jones, Jr. Pp. 1-356, plates 1-4, 82 figures in text. October 1, 1964. $3.50.
2. Synopsis of the lagomorphs and rodents of Korea. By J. Knox Jones, Jr., and David H. Johnson. Pp. 357-407. February 12, 1965.
3. Mammals from Isla Cozumel, Mexico, with description of a new species of harvest mouse. By J. Knox Jones, Jr., and Timothy E. Lawlor. Pp. 409-419, 1 figure in text. April 13, 1965.
4. The Yucatan deer mouse, Peromyscus yucatanicus. By Timothy E. Lawlor. Pp. 421-438, 2 figures in text. July 20, 1965.

More numbers will appear in volume 16.

Vol. 17. 1. Localities of fossil vertebrates obtained from the Niobrara Formation (Cretaceous) of Kansas. By David Bardack. Pp. 1-14. January 22, 1965.
2. Chorda tympani branch of the facial nerve in the middle ear of tetrapods. By Richard C. Fox. Pp. 15-21. June 22, 1965.

More numbers will appear in volume 17.

INDEX TO VOLUME 15

New systematic names are in **boldface** type

Abronia deppei, 683, 684
abscondens, Chiropterotriton, 187
Acacia, 646
  cymbispina, 643, 644
Acanthocereus pentagonus, 644
Acarina, 729
achilles, Anolis, 196
Achras zapote, 210
acridid, 397
Acris crepitans, 397, 514
Acrodytes inflata, 45
acutirostris, Geophis, 202
acutus, Crocodylus, 58, 653, 660, 679, 699
adipoventris, Ptychohyla, 314
aemula, Rhadinea, 683, 685
aeneus,
  Oxybelis, 104, 241, 609, 654, 656, 666, 679
  Sceloporus, 66, 653, 657, 658, 662, 665, 681, 682, 684, 690, 700
aequalis, Pliocercus, 242
aequatus, Zeugorchis, 547
aequifasciatus, Oxyrhophus, 246
affinis,
  Micrurus, 244, 611
  Pituophis, 36
Agalychnis
  alcorni, 44, 189
  dacnicolor, 44
  saltator, 189, 195
Agelaius phoeniceus, 398
Agkistrodon
  bilineatus, 120, 611, 655, 679
  blomhoffi, 170
  brevicaudus, 170
  contortrix, 396, 398
  halys, 168, 170
agkistrodontis, Kalicephalus, 444
ahaetulla, Leptophis, 241
Ahaetulla diplotropis, 103
alata, Crescentia, 643
alba, Tyto, 440
albida, Hyptis, 646
albolabris,
  Microbatrachylus, 34
  Tomodactylus, 682, 685
albomaculata, Cochranella, 190
alcorni,
  Agalychnis, 44, 189
  Phyllomedusa, 44
alfreddugèsi, Trombicula, 442, 547, 725, 728
alfredi, Eleutherodactylus, 586, 611
alcastrum, Brosimum, 210, 645
alienus, Micrurus, 611
alleei, Hyla, 342
alleni,
  Micrurus, 202
  Oedipina, 188
allisoni, Anolis, 196
Alnus arguta, 648
Alopoglossus plicatus, 196
alpestris, Otocoris, 397
altamontana, Pseudoeurycea, 682, 684
altamontanus, Rhadinaea, 203
altimirani,
  Eumeces, 78, 653, 659, 680, 701
  Rhyacosiredon, 682, 684
alvaradoi,
  Bolitoglossa, 187
  Hyla, 192
amblycephala, Ambystoma, 14
amblycephalum, Ambystoma, 14, 652, 682, 684
Amblycorypha inasteca, 400
Ambrosia trifida, 505
Ambystoma
  amblycephala, 14
  amblycephalum, 14, 652, 682, 684
  dumerili, 15, 652, 664, 686
  maculatum, 516
  ordinaria, 15
  ordinarium, 15, 652, 658, 662, 682
  tigrinum, 17, 652, 660, 661, 685, 718
  utahense, 718
  velasci, 17, 652, 660, 661, 685
Ameiva
  edwardsi, 212, 237
  festiva, 196, 212, 237
  gaigeae, 603
  hartwegi, 603
  occidentalis, 196
  sinistra, 80, 653
  undulata, 80, 212, 603, 653, 656, 660, 666, 679
Amelanchier utahensis, 729
americana, Schistocerca, 400
americanus,
  Bufo, 514, 516
  Fraxinus, 505
  Prunus, 505

amoenus, Carphophis, 396
Amphibians and reptiles from the Yucatan Peninsula, Mexico, 577
of Mesa Verde National Park, Colorado, 711
of the rainforests of southern El Peten, Guatemala, 205
Amphiesma
ruthveni, 155
vibakari, 165
amulae, Tomodactylus, 40
amurensis, Rana, 160
Anadia
arborea, 196
attenuata, 196
metallica, 196
anatina, Physa, 443
andrewsi, Pliocercus, 609
Ancisdron bilineatus, 120
Andropogon gerardi, 505
Anguis platura, 119
angustatus, Claudius, 230
angusticeps,
Bufo, 23
Cnemidophorus, 212, 604
angustidigitorum, Tomodactylus, 39, 652, 657, 660, 682, 684, 686, 701
angustipons, Kinosternon, 617
annectens, Tropidoclonion, 204
annellatus, Pliocercus, 203
annulata, Leptodeira, 680, 698
annulatus,
Chersodromus, 683, 685
Scaphiodontophis, 246
annuus, Helianthus, 505
anomala, Elaphe, 168
anomalum, Lepidophyma, 199
anomalus, Coluber, 168
Anono purpurea, 645
Anoplarchus purpurescens, 517
Anthicidae, 729
anthicus, Coluber, 356, 374
Anthocoridae, 729
anzuetoi, Eleutherodactylus, 222
Anolis
achilles, 196
allisoni, 196
aquaticus, 197
attenuatus, 197
biporcatus, 212, 234, 595
biscutiger, 197
bourgeaei, 213, 234, 595
capito, 212, 233
dunni, 60, 653, 682
gadowi, 680
humilis, 197, 213, 233, 595, 612
lemurinus, 213, 234, 595
limnifrons, 213, 234, 595
liogaster, 682, 685
marsupialis, 197
microlepidotus, 682, 685
nebulosa, 61
Anolis—*Concluded*
nebulosus, 61, 653, 655, 656, 657, 658, 659, 662, 663, 679, 686
nelsoni, 197
omiltemanus, 683, 685
rodriguezi, 213, 234, 595
sagrei, 596
schmidti, 63, 653, 660, 679
sericeus, 212, 234, 596
subocularis, 680
taylori, 680
tropidonotus, 212, 597
uniformis, 212, 213, 595, 612
ustus, 596
woodi, 197
Aphidae, 729
apiatus, Micrurus, 244
Apodemus, 168
Apoplanesia paniculata, 643, 644
Aporocactus, 645
approximans, Holbrookia, 721
aquaticus,
Anolis, 197
Scalopus, 397, 401
aquilus, Crotalus, 123, 655
aquilnaria, Geophis, 202
Araneida, 725, 729
arborea,
Anadia, 196
Hyla, 156
Licania, 645
arborescandens,
Bolitoglossa, 187
Hyla, 473
arboricola, Hyla, 682, 685
Arbutus xalapensis, 648
Archeology of Mesa Verde, 714, 715
Arctostaphylos viscida, 435
Ardea herodias, 546
arenicolor, Hyla, 46, 652, 664, 666, 682, 684, 686
areolata, Geoemyda, 592
argentea, Crysophila, 210
argus, Eremias, 162
arguta, Alnus, 648
Arid tropical scrub forest, 12, 643
Arion, 516
Aristelliger
georgeensis, 593
nelsoni, 197
Aristida, oligantha, 505
Arizona lineaticollis, 105
Arphia simplex, 403, 406
Artemisia tridentata, 724
asio, Phrynosoma, 65, 653, 679
asper,
Bothrops, 245, 611
Sceloporus, 66, 653, 667, 682, 699
Aspidonectes sinensis, 161
assata, Scincella, 77, 653, 656, 663, 679
assatum, Leiolopisma, 77

assimilis, Gryllus, 396, 400
Aster sp. 505
Astianthus viminalis, 645
Atelopus
  loomisi, 189, 190
  varius, 190
ater, Trionyx, 195
atomaria, Cassia, 644
atropurpureus, Xiphigaster, 517
atrox, Bothrops, 245, 611
attenuata, Anadia, 196
attenuatus,
  Anolis, 197
  Ophisaurus, 398, 403, 439
augusti, Eleutherodactylus, 37, 652, 682, 684, 699
aurata, Murina, 168
auratus,
  Dryinus, 104
  Oxybelis, 104, 609, 654
aurantiaca, Jaquinia, 644
auriceps, Crotaphytus, 198, 721
australis, Masticophis, 104
Avicenna nitida, 649
azteca, Hyla, 51

bairdi, Salvadora, 108, 655, 657, 663, 685
bakeri, Geophis, 202
bakewelli, Leptotyphlops, 89, 654
Balsas-Tepalcatepec Basin, 10
barbouri, Bothrops, 683, 685
barn owl, 441
basilisca, Caudisona, 120
basiliscus, Crotalus, 120, 655, 656, 679
Basiliscus vittatus, 64, 215, 216, 234, 597, 653, 655, 656, 664, 679
Bathysiredon dumerili, 15
baudini,
  Hyla, 46, 652, 655, 656, 679
  Smilisca, 228, 589
belli,
  Pseudoeurycea, 17, 652, 657, 658, 660, 681, 682, 684, 690
  Spelerpes, 17
Berg, Barbara with Duellman, William E. Type specimens of amphibians and reptiles in the Museum of Natural History, the University of Kansas, 183
berus, Vipera, 665
Bibionidae, 729
bicarinatus, Urosaurus, 75, 653, 679, 686
bicolor,
  Geophis, 683
  Loxocemus, 89, 654, 679
bilineatus,
  Ancisdrodon, 120
  Agkistrodon, 120, 611, 655
  Eumeces, 198
bilobatus, Gammarotettix, 397
biotic province, of Mesa Verde, 713
Bipes
  canaliculatus, 127, 653, 680, 701
  tridactylum, 680
biscutata,
  Dipsas, 111
  Trimorphodon, 111
biscutatus, Trimorphodon, 111, 655, 656, 660, 679
biscutiger, Anolis, 197
bisecta, Leposoma, 200
biserialis, Conopsis, 92, 654, 657, 658, 660, 681, 683, 684, 700
bislineata, Eurycea, 516
bistincta, Hyla, 47, 340, 469, 475, 652, 657, 658, 660, 664, 682, 684, 699
bivitellobata, Oochoristica, 728, 733
bivittatus, Melanoplus, 397, 400, 403
bivocata, Hyla, 192, 336
blanchardi,
  Lampropeltis, 608
  Opheodrys, 735
Blarina brevicauda, 396, 442, 516
blomhoffi, Agkistrodon, 170
Boa
  constrictor, 90, 237, 605, 654, 660, 679
  imperator, 90, 237, 605, 654
bocourti, Tantilla, 110, 655, 681, 683, 684
bogerti, Ptychohyla, 316
Bolitoglossa
  alvaradoi, 187
  arborescandens, 187
  dofleini, 215, 219
  mexicana, 586, 611
  moreleti, 215, 220, 586
  mulleri, 215, 220, 586
  odonelli, 586
  palustris, 187
  veracrucis, 187
Bombax ellipticum, 210, 645
Bombina orientalis, 153
Bombyliidae, 729
bonitaensis, Oedipina, 188
borealis,
  Kaloula, 156
  Quercus, 505
Bothrops
  asper, 245, 611
  atrox, 245, 611
  barbouri, 683, 685
  nasutus, 245
  nummifer, 245
  schlegeli, 201, 212, 245
  supraciliaris, 201
  undulatus, 683
  yucatanensis, 611
bourgeaei, Anolis, 234, 595
Bouteloua, 646
box turtle, ornate, 720
brachycephala,
  Plectrohyla, 195
  Rana, 720

brachypoda, Mabuya, 77, 200, 246, 603, 653, 660, 679
brachyrhynchos, Corvus, 441
brachystoma, Thamnophis, 505
Braconidae, 729
braminus, Typhlops, 88, 654
brasilletto, Haematoxylon, 645
brasiliense, Calophyllum, 210
Breeding cycle in the ground skink, Lygosoma laterale, 565
brevicauda, Blarina, 396, 442, 516
brevicaudus, Agkistrodon, 170
bressoni,
  Leptodeira, 103
  Leptotyphlops, 89, 654, 680, 701
brevifacies, Dipsas, 606
brevipes, Daihinia, 400, 403
brevirostris, Eumeces, 128, 198, 681, 682
Bromus inermis, 505
Brongniartia inconstans, 646
Brosimum alicastrum, 210, 645
browni, Micrurus, 683, 685
bufo, Bufo, 154
Bufo
  americanus, 514, 516
  angustipes, 23
  bufo, 154
  coccifer, 21, 652
  compactilis, 22, 652, 655, 657, 660, 685
  gargarizans, 154
  gemmifer, 680
  holdridgei, 190
  horribilis, 23
  lentiginosus, 397
  marinus, 23, 215, 587, 652, 656, 660, 679
  marmoreus, 23, 652, 655, 669, 679
  occidentalis, 29, 652, 657, 658, 682, 684, 686, 699
  perplexus, 29, 652, 659, 680, 701
  punctatus, 719, 733
  terrestris, 394, 405
  valliceps, 221, 587
  woodhousei, 514, 720
bulleri, Sceloporus, 66, 653, 658, 660, 667, 682, 690, 700
bunkeri, Holbrookia, 199
bursa, genital, in snakes, 362
Bursera
  jorullensis, 644
  microphylla, 646
  odorata, 646
  simaruba, 645
  sphaerocarpa, 644
Buteo
  jamaicensis, 439
  lineatus, 440
  platypterus, 440, 544
  swainsoni, 544
butleri, Thamnophis, 505
Butorides virescens, 546
Byers, George W., J. Knox Jones, Jr., with Robert G. Webb, Some reptiles and amphibians of Korea, 149

cactorum, Eleutherodactylus, 37, 652
caecilians, 186
caerulea, Uta, 201
coeruleus, Urosaurus, 201
Caesalpina, platyloba, 644
Caiman crocodilus, 126
calamarina, Tantilla, 110, 655, 660, 680
calcitrans, Eleutherodactylus, 682, 685
calidipes, Cnemidophorus, 81, 653, 659, 662, 666, 680, 701
californicus, Microtus, 397
callicephalus, Eumeces, 128
callidryas, Phyllomedusa, 212, 226, 589
calligaster,
  Lampropeltis, 397, 439
  Sceloporus, 71
calophylla, Quercus, 648
Calophyllum brasiliense, 210
Calosoma scrutator, 401, 442
calvatus, Trionyx, 196
calyculata, Euphorbia, 646
Campanotus vicinus, 725, 728
canaliculatus, Bipes, 127, 652, 680, 701
canadensis, Cercis, 505
Canavalia maritima, 649
canescens, Thamnophis, 118
Canoula pellucida, 397
canula, Tantilla, 610
capiri, Sideroxylon, 645
caprimimus, Hypopachus, 52, 652, 659, 669, 680, 686, 701
Carabidae, 725
cardinalis, Richmondena, 398
Caretta caretta, 590
carinata, Neduba, 397
carolina,
  Dissosteira, 396, 397, 398
  Terrapene, 396, 405
Carphophis amoenus, 396
carpicinctus, Scaphiodontophis, 246
Casearia sp., 210
Cassia
  atomaria, 644
  emarginata, 644
Castilla elastica, 210, 645
catenatus, Sistrurus, 381
catesbeiana, Rana, 397, 516
Caudata, 186
Caudisona
  basilisca, 120
  polysticta, 122
Cauphias
  crassum, 486
  crassus, 486
  guatemalensis, 488

Ceanothus cuneatus, 435
Cecidomyidae, 729
Cecropia mexicana, 210
Cedar Bluff Reservoir, 355
Cedrela mexicana, 210
Ceiba
  parvifolia, 645
  pentandra, 210
celaenops, Lampropeltis, 737
Celtis iguanaea, 644
cenchoa, Imaneodes, 212, 239, 607
Central America, a new species of turtle, genus Kinosternon, 615
Centrolenella spinosa, 190, 195
cephalica, Pseudoeurycea, 684
Cercidium plurifoliolatum, 643, 644
Cercis canadensis, 505
Cercocarpus montanus, 729
cerroensis,
  Magnadigita, 187
  Ninia, 203
Ceuthophilus sp., 396
Chalcidae, 729
chamulae, Ptychohyla, 195, 306, 333, 334
chaneque, Hyla, 193, 336
charadricola, Hyla, 473, 478
Chelonia mydas, 56, 590
Chelydra rossignovi, 215, 230
cherriei,
  Leiolopisma, 199, 201
  Scincella, 199, 201, 236, 603
Chersodromus annulatus, 683, 685
chihuahuaensis, Thamnophis, 204
chilensis, Prosopis, 644
Chiropterotriton
  abscondens, 187
  chiropterus, 684
chiropterus, Chiropterotriton, 684
chirripoi, Cochranella, 190
Chloropidae, 729
Chortophaga viridifasciata, 397, 398, 400
chosenica, Rana, 159
Chrysemys picta, 397, 405
chrysocephalus, Thamnophis, 683
Chrysomelidae, 725, 728, 729
Chrysopidae, 729
chrysostictus, Sceloporus, 601
Cicadellidae, 725, 728, 729
cinerea, Hyla, 396
cinereus, Plethodon, 516
Cinosternon hirtipes, 57
Circus cyaneus, 439
clamitans, Rana, 396, 516
clarki, Enyaliosaurus, 65, 653, 656, 659, 660, 663, 680
Claudius angustatus, 230
clavatus, Coniophanes, 238, 605
clelia, Clelia, 237, 654, 679
Clelia clelia, 237, 654, 679
Clethrionomys gapperi, 396
Clistogastra, 729
Cnemidophorus
  angusticeps, 212, 604
  calidipes, 81, 653, 659, 662, 666, 680, 701
  communis, 81, 653, 660, 668, 680
  costatus, 83, 653, 659, 668, 686, 701
  cozumelae, 604
  deppei, 84, 654, 660, 668
  exoristus, 85, 654
  guttatus, 680, 698
  infernalis, 84, 654
  lineatissimus, 85, 654, 656, 666, 668 680, 698, 701
  lividus, 86, 654
  occidentalis, 83
  parvisocius, 701
  rodeki, 604
  sacki, 680
  scalaris, 86, 402, 654, 657, 660, 685
  sexlineatus, 396, 398, 403, 404
  velox, 731, 732, 733
  zweifeli, 83, 654
coccifer, Bufo, 21, 652
Coccinellidae, 725
Coccoloba uvifera, 645
Cochranella
  albomaculata, 190
  chirripoi, 190
  colymbiphyllum, 190
  decorata, 190, 191
  millepunctata, 190
  reticulata, 191
  talamancae, 191
  viridissima, 682, 684
Cocos nucifera, 649
coeruleus, Gerrhonotus, 398
cohune, Orbigyna, 210, 649
Coleonyx
  elegans, 127, 215, 232, 594, 653, 697
  nemoralis, 127, 653
colimensis, Eumeces, 78, 653, 656, 679
collared lizard, 721
collaris,
  Crotaphytus, 198, 395, 397, 720, 721, 728
  Sibynophis, 203
Colubridae, 255
Colubrina heteroneura, 644
Coluber, 166
  anomalus, 168
  anthicus, 356, 374
  constrictor, 353, 381, 396
  dione, 167
  doliatus, 101
  flaviventris, 376, 398, 413, 419, 420, 423
  foxi, 357
  helvigularis, 371, 374
  mormon, 356, 374, 375, 376, 413, 419, 420, 423, 440

Coluber—*Concluded*
nebulatus, 109
oaxacae, 371
paludicola, 371
priapus, 371, 374, 375, 419
spinalis, 371
stejnegerianus, 372, 374, 375, 419
striolatus, 104
colubrinus,
Ophis, 290
Xenodon, 290
colymbiphyllum, Cochranella, 190
communis,
Cnemidophorus, 81, 653, 660, 668, 680
Commelina, 505
compactilis, Bufo, 22, 652, 655, 657, 660, 685
concolor,
Conophis, 270, 606
Crotalus, 737
conica, Toluca, 683
Coniophanes, 256
bipunctatus, 215, 238
clavatus, 215, 218, 605
dispersus, 91, 654
fissidens, 91, 201, 215, 238, 654, 679
imperialis, 215, 238, 272, 605
lateritius, 91, 654, 680, 699
meridianus, 605
obsoletus, 201
schmidti, 605
Conocarpus erecta, 649
Conocephalus sp., 400
Conophis
concolor, 270, 606
dunni, 262
lineaticeps, 270
lineatus, 212, 262, 267, 606
nevermanni, 264, 272
plagosus, 264
pulcher, 274
similis, 274
viduus, 279
vittata, 278
vittatus, 91, 277, 654, 679
Conopsis
biserialis, 92, 654, 657, 658, 660, 681, 683, 684, 700
nasus, 92, 654, 660, 683, 700
consors, Kinosternon, 591
constrictor,
Boa, 605
Coluber, 381, 396, 413, 420, 440
Contia michoacanensis, 109
contortrix, Agkistrodon, 396, 398
cooperi, Synaptomys, 397
copei, Eumeces, 79, 653, 683, 684, 700
corais, Drymarchon, 93, 239, 654, 656, 660, 679, 686
corasterias, Phrynohyas, 45
Cordia
dentata, 644
eleganoides, 644
Cordillera Volcanica, 10
coreana, Rana, 160
Coreidae, 729
Cornus, 643
drummondi, 505
coronadoi, Tantilla, 683, 685
Corvus brachyrhynchos, 441
Corythophanes
cristatus, 235
hernandezi, 598
costaricense, Dermophis, 186
costaricensis,
Dipsas, 201
Tantilla, 203
costatus, Cnemidophorus, 83, 653, 659, 668, 686, 701
coulteri, Guaiacum, 643
coyote, 441
cozumelae, Sceloporus, 602
cozumelas, Cnemidophorus, 604
crassa,
Hyla, 473, 486
Plectrohyla, 487
crassidigitatus, Eleutherodactylus, 191
crassifolia, Quercus, 648
crassum, Cauphias, 486
crassus,
Cauphias, 486
Hypsiboas, 487
Crataegus sp., 435
creaseri, Kinosternon, 590
Crematogaster lineolata, 725, 728, 729
crepitans,
Acris, 397, 514
Hura, 645
Crescentia alata, 643
crocodilus, Caiman, 126
Crocodylus
acutus, 58, 653, 660, 679, 699
moreleti, 215, 229, 593
Crotalus
aquilus, 123, 655
basiliscus, 120, 655, 656, 679
concolor, 737
culminatus, 121, 655
durissus, 121, 611, 655
horridus, 439
intermedius, 121, 655, 681, 683
molossus, 121, 655, 659, 660, 681, 683
nigrescens, 121, 655
nuntius, 737
polystictus, 122, 655, 660
pusillus, 122, 655, 657, 658, 660, 683
transversus, 683
triseriatus, 123, 655, 657, 662, 665, 681, 683, 684

Crotalus—*Concluded*
tzabcan, 611
viridis, 737
Crotaphytus, 725
auriceps, 198, 721
collaris, 198, 395, 397, 720, 721, 728
crow, 441
crucifer, Hyla, 396, 516
cruentatum, Kinosternon, 591
crus-galli, Echinochloa, 505
Cryptotis parva, 401, 403, 442
Crysophila argentea, 210
Ctenosaura
pectinata, 64, 653, 655, 656, 660, 663, 679
similis, 212, 598
culminatus, Crotalus, 121, 655
cuneatus, Ceanothus, 435
cuneus, Hypopachus, 229, 589
cuniculator, Tantilla, 610
curculionid, 403
Curculionidae, 725, 728
curinus, Zeugorchis, 547
cyaneus, Circus, 439
cyanosticta, Smilisca, 229
Cyclura pectinata, 64
cyclides, Thamnophis, 114, 117
cyclocarpum, Enterolobium, 644, 645
cyclocauda, Oedipina, 188
cyclomaculata, Hyla, 193, 473
Cyclorrhapha, 725
cymbispina, Acacia, 643, 644
Cymbopetalum penduliflorum, 210
Cynipidae, 729
Cyrtocarpa procera, 644
cyrtopsis, Thamnophis, 114, 117, 507, 518
Cystignathus
labialis, 30
melanotus, 30

dacnicolor,
Agalychnis, 44
Phyllomedusa, 44, 189, 652, 656, 660, 662, 664, 679
Daihinia brevipes, 400, 403
dalquesti, Hyla, 193, 194, 473
Dasymetra longicirrus, 547
debilis, Hyla, 193
deborrei, Laemanctus, 235, 600, 612
decipiens,
Quercus, 648
Rhadinaea, 203
decorata,
Cochranella, 190, 191
Rhadinaea, 246
decticids, 397
defensor, Enyaliosaurus, 598, 701
degenhardti, Stenorrhina, 243
dekayi, Storeria, 397, 517
delcampi, Phyllodactylus, 680
dentata, Cordia, 644
Dendrobates granuliferus, 191
Dendroscarta, Hyla, 326
deppei,
Abronia, 683, 684
Cnemidophorus, 84, 654, 660, 668, 701
Pituophis, 105, 655, 657, 661, 685
Tantilla, 683
Dermatemys mawi, 215, 231
Dermophis
costaricensis, 186
glandulosus, 186
mexicanus, 246
multiplicatus, 680, 698
occidentalis, 186
Deroceras, 516
desert striped whip snake, 734
deserticola, Pituophis, 735
Desmognathus fuscus, 516
devastator, Melanoplus, 397, 403
diademata, Ninia, 246
Diadophis
dougesii, 92
dugesi, 92, 654, 660
dugesii, 92
punctatus, 92, 381, 401
dicei, Eumeces, 198
Didalium guianense, 210
differentialis, Melanoplus, 398, 400, 403
dilatus, Tomodactylus, 682, 685, 701
dimidiata, Sibon, 243
dioica,
Gymnocladus, 505
Hasseltia, 210
dione,
Coluber, 167
Elaphe, 167
Elaphis, 167
Diphysa floribunda, 644
diplotropis,
Ahaetulla, 103
Leptophis, 103, 654, 656, 659, 662, 666, 679
Dipsas
biscutata, 111
brevifacies, 606
costaricensis, 201
gemistratus, 101
latistrata, 101
tenuissima, 201
dispersus, Coniophanes, 91, 654
Dissosteira carolina, 396, 397, 398
distachya, Mimosa, 643
distans, Micrurus, 118, 655, 656, 659, 660, 680, 699
distribution of herpetofauna of Michoacan, 677
dofleini, Bolitoglossa, 215, 219
doliata, Lampropeltis, 101, 202, 240, 608, 654, 683, 685, 687, 701, 737
doliatus, Coluber, 101

dorsalis,
Rhinophrynus, 20, 212, 586, 652, 660, 679, 699
Thamnophis, 117, 655, 657, 658, 659, 666, 681, 683, 684, 699
dougesii, Diadophis, 92
Douglas, Charles L.
Amphibians and reptiles of Mesa Verde National Park, Colorado, 711
douglassi, Phrynosoma, 731, 734
Dromicus
laureatus, 107
putnami, 104
taeniatus, 107
drummondi, Cornus, 505
Dryadophis
laevis, 238
melanolomus, 93, 238, 606, 654, 656, 660, 666, 679, 699
sanguiventris, 201
stuarti, 93, 654
Dryinoides, 293
Dryinus auratus, 104
Drymarchon
corais, 93, 239
melanurus, 239
rubidus, 93
Drymobius
fistulosus, 94, 654
margaretiferus, 94, 213, 216, 239, 606, 654, 655, 656, 660, 666, 679
dubitus, Eleutherodactylus, 192
Duellman, W. E.
A biogeographic account of the herpetofauna of Michoacan, Mexico, 627
A review of the frogs of the Hyla bistincta group, 469
A review of the Middle American tree frogs of the genus Ptychohyla, 297
Amphibians and reptiles from the Yucatan Peninsula, Mexico, 577
Amphibians and reptiles of the rain forests of southern El Peten, Guatemala, 205
The amphibians and reptiles of Michoacan, Mexico, 1
Duellman, William E. and Barbara Berg
Type specimens of amphibians and reptiles in the Museum of Natural History, The University of Kansas, 183
duellmani, Phyllodactylus, 59, 653, 656, 659, 660, 662, 680, 701
Duges, Alfredo, 7
dugesi,
Eumeces, 79, 653, 657, 658, 660, 681, 683
dugesi—*Concluded*
Sceloporus, 67, 653, 657, 661, 663, 667, 685
dugesii,
Diadophis, 92, 654, 660
Geophis, 96, 654, 686
dulcensis, Hyla, 193
dumerili,
Ambystoma, 15, 652, 664, 686
Ambystoma (Bathysiredon), 15
Bathysiredon, 15
Dumerili, Siredon, 15
dunni,
Anolis, 60, 653, 682
Conophis, 262
Kinosternon, 621
Rana, 54, 652, 657, 686, 701
durangoensis, Eumeces, 198
durissus, Crotalus, 121, 611, 655
dybowskii, Rana, 161

earless lizard, speckled, 721
ebbracata, Hyla, 212, 223
echinatum, Pithecotenium, 644
Echinochloa crus-galli, 505
edulis, Pinus, 729
edwardsi, Ameiva, 212, 237
Elaphe
anomala, 168
dione, 167
flavirufa, 606
guttata, 381
intermedia, 95
intermedius, 654
mutabilis, 246
obsoleta, 401, 438, 544
rufodorsata, 157, 167
triaspis, 95, 246, 607, 654, 657, 686
Elaphis dione, 167
elapoides, Pliocercus, 246
elastica, Castilla, 210, 645
elaterid, 403
eleganoides, Cordia, 644
elegans,
Coleonyx, 127, 215, 232, 594, 653, 679
Gastrophryne, 246, 589
Micrurus, 247
Thamnophis, 438, 733
Eleutherodactylus, 488
alfredi, 586, 611
anzuetoi, 222
augusti, 37, 652, 682, 684, 699
cactorum, 37, 652, 682, 684, 699
calcitrans, 682, 685
crassidigitatus, 191
dubitus, 192
gollmeri, 222
minimus, 192
occidentalis, 37, 652, 656, 686
persimilis, 192, 194

Eleutherodactylus—*Concluded*
rhodopis, 222
rostralis, 215, 222
rugulosus, 38, 223, 652, 656, 664, 666, 679
saltator, 682, 685
taurus, 192
vocalis, 38, 652, 656, 664, 666, 679
vocator, 192
ellipticum, Bombax, 210, 645
ellipticus, Renifer, 444
elongatus, Sceloporus, 725
emarginata, Cassia, 644
Emys
ornata, 126
pulcherrima, 125
Engystomops pustulosus, 587
Enterolobium cyclocarpum, 644, 645
Enulius unicolor, 654, 656, 663, 683, 684
Enyaliosaurus
clarki, 65, 653, 656, 660, 663, 669, 680, 701
defensor, 598, 701
quinquecarinatus, 701
epipleurotis, Eumeces, 198
eques, Thamnophis, 117, 655, 657, 661, 685
erecta, Conocarpus, 649
Eremias argus, 162
Eretmochelys imbricata, 590
Erythraeidae, 729
Erythrolamprus, 256
erythromma, Hyla, 326, 682
Erythroxylon pallidum, 644
Eumeces
altimirani, 7, 78, 653, 659, 680, 701
bilineatus, 198
brevirostris, 128, 198, 681, 683
callacephalus, 128
callicephalus, 128
colimensis, 78, 653, 656, 679
copei, 79, 653, 683, 684, 700
dicei, 198
dugesi, 79, 653, 657, 658, 660, 681, 683
durangoensis, 198
epipleurotis, 198
fasciatus, 420
gaigei, 198, 733
indubitus, 79, 653, 681, 683, 700
inexpectatus, 198
lynxe, 198
multivirgatus, 198, 733
obsoletus, 395, 402, 403
ochoterenai, 683
parvulus, 80, 653, 656, 679
pineus, 198
schwartzei, 212, 236, 603, 701
skiltonianus, 397
sumichrasti, 212, 236
taylori, 198
Eunulius unicolor, 95
Euphorbia calyculata, 646
Eurycea bislineata 516
euryzonus, Pliocercus, 242
euthysanota,
Hyla, 301, 315
Ptychohyla, 302, 303, 304, 315, 316
Eysenhardtia, 646
eximia, Hyla, 49
exoristus, Cnemidophorus, 85, 654

Fagus, 643
Falco sparverius, 440, 544
fasciata, Tropidodipsas, 129, 610
fasciatus,
Eumeces, 420
Nemobius, 396
femoralis, Hyla, 396
femur-rubrum, Melanoplus, 396
Fendlera rupicola, 729
festiva, Ameiva, 196
Ficimia
publia, 607, 680, 698
streckeri, 202
Ficus, 210, 644
mexicana, 645
padifolia, 645
Fir forest, 12, 648
fissidens, Coniophanes, 91, 201, 215, 238, 654, 679
fistulosus, Drymobius, 94, 654, 655, 656, 660, 679
Fitch, Henry S.
An ecological study of the garter snake, Thamnophis sirtalis, 493
Natural History of the racer, Coluber constrictor, 351
Fitch, Henry S. and Greene, Harry W.
Breeding cycle in the ground skink, Lygosoma laterale, 565
fitzingeri,
Elaps, 129
Micrurus, 129
flagellum, Masticophis, 397
flavimaculatum, Lepidophyma, 215, 236
flavirufa, Elaphe, 606
flaviventris, Coluber, 376, 398, 413, 419, 420, 423
flavomarginatus, Gopherus, 195
floribunda, Diphysa, 644
floridanus, Sylvilagus, 397, 401, 544
fodiens, Pternohyla, 44, 652, 680
fontinalis, Salvelinus, 517
forest,
arid tropical scrub, 643
fir, 12, 648
pine-oak, 647
tropical semi-deciduous, 644
Formicidae, 725, 728, 729
formosa, Fouquieria, 646
formosus, Sceloporus, 682, 684
Fouquieria formosa, 646
foxi, Coluber, 357

freminvilli, Stenorhina, 610, 680, 698
frenata, Leptodeira, 240, 608
frenatus, Hemidactylus, 680
frog, a new species of (genus Tomodactylus) from western Mexico, 175
western leopard, 720
frontalis,
Pseudoficimia, 105, 655, 659, 699, 701
Toluca, 105
Fraxinus americanus, 505
fulgidus, Oxybelis, 609
Fulgoridae, 729
fuscus,
Caiman, 126
Desmognathus, 516
Perosuchus, 126
Stenopelmatus, 397
Tomodactylus, 39, 652, 660, 682, 684

gabbi, Smilisca, 193
gadovi, Uta, 76
gadowi,
Anolis, 680
Gerrhonotus, 683
Leptotyphlops, 89, 654, 680, 701
Sceloporus, 68, 653, 656, 659, 663, 680, 701
Urosaurus, 76, 653, 663, 680, 701
gaigeae,
Ameiva, 603
Sceloporus, 602
gaigei, Eumeces, 198, 733
gairdnerii, Salmo, 517
gambelii, Quercus, 724, 726
Gammarotettix bilobatus, 397
gapperi, Clethrionomys, 396
gargarizans, Bufo, 154
garter snake, 495, 733
Gastrophryne
elegans, 246, 589
olivacea, 402, 514
usta, 652, 679
gaumeri, Heteromys, 290
gazetteer of southern El Petén, 210
Geagras redimitus, 96, 654, 660, 663, 679, 699
Geatractus techpanensis, 654, 679
Geckobiella texana, 725, 728
gemmifer, Bufo, 680
gemmistrata, Dipsas, 101
gemmistratus, Imantodes, 100, 654, 679
Geoemyda
areolata, 215, 231, 592
perixantha, 58, 653
pulcherrima, 125, 652, 679
rubida, 58, 652, 679
Geometridae, 729
Geophis
acutirostris, 202
aquilonaris, 202
Geophis—*Concluded*
bakeri, 202
bicolor, 683
dugesii, 96, 654, 686
incomptus, 97, 654, 658, 683, 684, 701
maculiferus, 97, 654, 669, 683, 684, 701
nigrocinctus, 97, 654, 658, 669, 683, 684, 701
omiltemanus, 683, 685
petersi, 98, 654, 657, 683, 699
tarascae, 98, 654, 669, 683, 684, 701
zeledoni, 202
georgeensis, Aristelliger, 593
georgianum, Neorenifer, 444
gerardi, Andropogon, 505
Gerrhonotus
coeruleus, 398
gadowi, 683
imbricatus, 87, 654, 658, 660, 662, 665, 681, 683
liocephalus, 683
multicarinatus, 397, 439, 665
getulus, Lampropeltis, 444
giganticus, Pharyngodon, 721, 725, 728, 729, 730, 733
glabra, Rhus, 505
glandulosus, Dermophis, 186
glaucus, Sphaerodactylus, 594
Gleditsia triacanthos, 505
Gobiesox meandricus, 517
godmani, Hyla, 323
gollmeri, Eleutherodactylus, 222
gopher snake, 735
Gopherus flavomarginatus, 195
gracilis, Oedipina, 188
gracillinus, Imantodes, 100
graciosus, Sceloporus, 398, 404, 720, 722, 726, 734
grammicus, Sceloporus, 69, 653, 658, 660, 662, 665, 666, 681, 682, 684
grandis, Tomodactylus, 682, 684
granuliferus, Dendrobates, 191
Great Basin
gopher snake, 735
sagebrush lizard, 722
Greene, Harry W. with Fitch, Henry S. Breeding cycle in the ground skink, Lygosoma laterale, 565
Gryllus
assimilis, 396, 400
pennsylvannicus, 396
Guaiacum coulteri, 643
Guatemala, amphibians and reptiles of the rainforests, 205
guatemalensis,
Cauphias, 488
Plectrohyla, 488
Guazuma ulmifolia, 644

guerreroensis, Tropidodipsas, 129
guianense, Didalium, 210
guttata, Elaphe, 381
guttatus, Cnemidophorus, 680, 698
Gymnocladus dioica, 505
Gymnophiona, 186

Haematoxylon brasiletto, 645
Haemorrhois, 371
Halictus sp., 725, 729
Haliplidae, 729
halys, Agkistrodon, 168
hammondi, Scaphiopus, 21, 652, 657, 660, 685, 740
harteri, Natrix, 203
hartwegi,
  Ameiva, 603
  Pinus, 648
Harvey County Park, 355, 384, 495
Hasseltia dioica, 210
Hayne method (of census), 553
hazelae, Hyla, 473
Helianthus annuus, 505
Heliosoma trivolvis, 443
Heloderma
  horridum, 87, 654, 660, 679, 684, 699
  suspectum, 194
helvigularis, Coluber, 371
Hemidactylus frenatus, 680
hernandezi, Corythophanes, 598
herodias, Ardea, 546
herpetofauna
  composition in Michoacan, 650
  distribution in Michoacan, 677
  ecology in Michoacan, 650
  geography in Michoacan, 673
  origin in Michoacan, 691
  rain forest of El Petén, 211
hesperia, Rhadinea, 106, 655, 656, 659, 668
Heterodon platyrhinos, 397
heterolepis,
  Notropis, 517
  Sceloporus, 653, 658, 681, 682, 700
Heteromys gaumeri, 289
heteroneura, Colubrina, 644
Hibiscus tiliaceus, 649
Hicoria ovata, 505
Hippiscus, 397
Hippodamia, 725
hirta, Trichilia, 645
hirtipes,
  Cinosternon, 57
  Kinosternon, 57, 653, 661, 685
hispidus, Sigmodon, 401, 544
hobartsmithi, Microbatrachylus, 33, 652, 657, 660, 681, 682
Holbrookia, 397
  approximans, 721
  bunkeri, 199
  maculata, 199, 398, 404, 721, 722
holdridgei, Bufo, 190
homolepidurus, Phyllodactylus, 59, 653, 656, 679
hondurensis, Scaphiodontophis, 246
horribilis, Bufo, 23
horridum, Heloderma, 87, 654, 660, 679
horridus,
  Crotalus, 439
  Sceloporus, 70, 653, 655, 656, 663, 679
humilis, Anolis, 197, 595, 612
Hura crepitans, 645
hydrography of Michoacan, 635
Hyla, 301
  alleei, 342
  alvaradoi, 192
  arborea, 156
  arborescandens, 473
  arboricola, 682, 685
  arenicolor, 46, 652, 664, 666, 682, 684, 686
  azteca, 51
  baudini, 46, 652, 655, 656, 679
  bistincta, 47, 340, 469, 475, 652, 657, 658, 660, 664, 682, 684, 699
  bivocata, 192, 336
  chaneque, 193, 336
  charadricola, 473, 478
  cinerea, 396
  crassa, 473, 486
  crucifer, 396, 516
  cyclomaculata, 193, 473
  dalquesti, 193, 194, 473
  debilis, 193
  dendroscarta, 326
  dulcensis, 193
  ebbracata, 212, 223
  erythromma, 326, 682
  euthysanota, 301, 315
  eximia, 49, 652, 657, 685
  femoralis, 396
  godmani, 323
  hazelae, 473
  immensa, 193
  japonica, 156
  labeculata, 475
  lafrentzi, 50, 652, 658, 682, 684, 690, 700
  legleri, 193, 342
  leonhardschultzei, 314
  leonhard-schultzei, 323
  loquax, 212, 225, 319, 588
  macrotympanum, 320
  manisorum, 193
  martini, 212, 225, 588
  melanomma, 326, 682, 685
  microcephala, 212, 225, 588, 652, 679
  microeximia, 49
  milleri, 324
  miotympanum, 323, 481
  mixomaculata, 193, 342
  moesta, 473

Hyla—*Concluded*
moraviensis, 194
pachyderma, 483, 485
picta, 226, 588
pinorum, 323
proboscidea, 194, 473
rickardsi, 319
rivularis, 194, 342
robertsorum, 473, 481
robustofemora, 487
rozellae, 316
rufioculis, 194, 342
salvadorensis, 341
sartori, 652, 674
smaragdina, 51, 652, 657, 662, 682, 686
smithi, 52, 652, 655, 656, 660, 679
staufferi, 194, 212, 226, 588, 680, 698
sumichrasti, 322
uranochroa, 342
versicolor, 397, 514
walkeri, 322
wellmanorum, 194, 195
weyerae, 194
Hylodes, 488
Hylodidae, 488
Hynobius leechii, 152
Hypopachus
caprimimus, 52, 652, 659, 669, 680, 701
cuneus, 229, 589
nigroreticulatus, 229, 589
ovis, 53, 652, 657, 660, 661, 668
oxyrrhinus, 53, 652, 657, 660, 661, 668
Hypsiboas crassus, 487
Hypsiglena
latifasciata, 102
loreala, 737
ochrorhyncha, 99, 654
torquata, 99, 100, 654, 657, 659, 680, 685, 699, 737
Hyptis albida, 646

Ichneumonidae, 729
ignicolor, Ptychohyla, 303, 337
iguana, Iguana, 64, 599, 653, 664, 679
Iguana
iguana, 64, 599, 653, 664, 679
rhinolopha, 64, 215, 216, 235, 599, 653
iguanaea, Celtis, 644
Imantodes
cenchoa, 212, 239, 607
gemmistratus, 100, 654, 679
gracillimus, 100, 654
latistratus, 101, 654
leucomelas, 212, 239, 607
tenuissimus, 607
imbricata, Eretmochelys, 590
imbricatus, Gerrhonotus, 87, 654, 658, 660, 662, 665, 681, 683
imitator, Microbatrachylus, 34
immensa, Hyla, 193
imperalis, Coniophanes, 272, 605
imperator, Boa, 90, 237, 605, 654
inasteca, Amblycorypha, 400
incomptus, Geophis, 97, 654, 658, 669, 683, 684, 701
inconstans, Brongniartia, 646
index, Lincoln, 551
indubitus, Eumeces, 79, 653, 681, 683, 700
inermis, Bromus, 505
inexpectatus, Eumeces, 198
infernalis, Cnemidophorus, 84, 654
inflata,
Acrodytes, 45
Phrynohyas, 45, 652, 660, 679
insignis, Lechriorchis, 547
integrum, Kinosternum, 58, 653, 659, 660, 664, 682, 686
intermedia, Elaphe, 95
intermedius,
Crotalus, 121, 655, 681, 683
Elaphe, 654, 657, 686
Pityophis, 95
Sceloporus, 67, 653
inusitata, Oedipina, 188
ioensis, Pyrus, 435
Ipomoea
murucordes, 646
pes-caprae, 649
isabelleae, Natrix, 133, 665
ixbaac, Scincella, 603

jamaicensis, Buteo, 439
japonica, Hyla, 156
Jaquinia
aurantiaca, 644
pungens, 644
Jones, J. Knox, Jr., George W. Byers, with Robert G. Webb. Some reptiles and amphibians from Korea, 149
jorullensis, Bursera, 644
juliflora, Prosopis, 643
Juniperus osteosperma, 729

Kalicephalus
agkistrodontis, 444
natricis, 164
rectiphilus, 444
Kaloula borealis, 156
kansensis, Trombicula, 442, 547
Kinosternon
acutum, 215, 230
angustipons, 617
consors, 591
creaseri, 590
cruentatum, 591
dunni, 621
hirtipes, 57, 653, 661, 685
integrum, 58, 653, 659, 660, 664, 682, 686
leucostomum, 215, 231, 592

labeculata, Hyla, 475
labialis,
Cystignathus, 30
Leptodactylus, 30, 223, 587, 652
Lacerta
orbiculare, 127
vivipara, 665
Laemanctus
deborrei, 235, 600, 612
serratus, 600
laevis, Dryadophis, 238
lafrentzi, Hyla, 50, 652, 658, 682, 684, 690
Lampropeltis
blanchardi, 608
calligaster, 397, 439
celaenops, 737
doliata, 101, 202, 240, 608, 654, 683, 685, 687, 701, 737
getulus, 444
polyzona, 215, 240
ruthveni, 102, 654, 661, 686, 701
taylori, 202
lampropholis,
Leiolopisma, 199, 201
Scincella, 199, 201
lanceolatum, Pithecollombium, 644
lanceolatus, Lonchocarpus, 645
lanei, Phyllodactylus, 59, 653, 656, 660, 679
Languncularia racemosa, 649
Lasius
neoniger, 725, 728, 729
niger, 725, 728, 729
laterale, Lygosoma, 396, 567
lateralis,
Rhabdophis, 164
Tretanorhinus, 244
lateriporus, Neorenifer, 443
lateritius, Coniophanes, 91, 654, 680, 699
laticollaris,
Elaps, 119
Micrurus, 119, 655, 656, 680, 699
latifascia, Trimorphodon, 111, 655, 656, 659, 680, 699
latifasciata,
Hypsiglena, 102
Leptodeira, 102, 654, 656, 659, 680, 699
latipes, Mocis, 401
latistrata, Dipsas, 101
latistratus, Imantodes, 100
laureata, Rhadinea, 107
laureatus, Dromicus, 107
lawsoni, Pinus, 648
Lechriorchis
insignis, 547
plesientera, 547
primus, 547
tygarti, 547
leechii, Hynobius, 152
Leersia oryzoides, 505
Legler, John M.
A new species of turtle, genus Kinosternon, from Central America, 615
legleri, Hyla, 193, 342
Leiolopisma
assatum, 77
cherriei, 199, 201
lampropholis, 199, 201
taylori, 77
leiophylla, Pinus, 648
lemniscata, Salvadora, 680
lemurinus, Anolis, 595
lentiginosus, Bufo, 397
leonhardschultzei,
Hyla, 314
Ptychohyla, 303, 323, 682
leonhard-schultzei,
Hyla, 324
Ptychohyla, 324
leopard frog, 720
Lepidochelys olivacea, 125
Lepidophyma
anomalum, 199
flavimaculatum, 215, 236
obscurum, 199
ophiophthalmum, 200
reticulatum, 200
Lepidoptera, 725, 728, 729
Leposoma
bisecta, 200
orientalis, 200
southi, 200
leprosa, Pseudoeurycea, 684
leprus, Syrrhophus, 223
Leptodactylidae, 488
Leptodactylus
labialis, 30, 223, 587, 652
melanonotus, 30, 223, 587, 652, 655, 656, 660, 679
occidentalis, 31, 652, 686
Leptodeira
annulata, 680, 698
bressoni, 103, 654
frenata, 240, 608
latifasciata, 102, 654, 656, 659, 680
maculata, 102, 654, 656, 660, 680, 698
malleisi, 240, 608
nigrofasciata, 680
polysticta, 128, 240, 654
septentrionalis, 128, 240, 654, 679
splendida, 103, 654, 659, 680, 699
torquata, 100
yucatanensis, 608
Leptophis
ahaetulla, 212, 241
diplotropis, 103, 654, 656, 659, 662, 666, 679
mexicanus, 241, 608, 680, 698
praestans, 241

Leptotyphlops
bakewelli, 89, 654
bressoni, 89, 654, 680, 701
gadowi, 89, 654, 680, 701
phenops, 89, 654, 663, 679, 701
Lespedeza striata, 505
leucomelas, Imantodes, 239, 607
Leucopremna mexicana, 645
leucopus, Peromyscus, 396, 401, 403, 443, 514
leucostomum, Kinosternon, 592
Licania arborea, 645
limnifrons, Anolis, 595
lineata,
Tachymenis, 267
Toluca, 110, 655, 657, 658, 660, 683, 684
lineaticollis,
Arizona, 105
Pituophis, 105, 655, 657, 658, 683, 684, 686, 699
lineatissimus, Cnemidophorus, 85, 654, 656, 666, 668, 680, 698, 701
lineatum,
Tomodon, 262, 267
Tropidoclonion, 204
lineatus,
Buteo, 440
Conophis, 212, 262, 267, 606
Psammophis, 262
lineolata, Crematogaster, 725, 728, 729
liogaster, Anolis, 682, 685
liocephalus, Gerrhonotus, 683
Liolepisma laterale, 163
Liopeltis vernalis, 396
lipovskyana, Trombicula, 442, 547
Liquidambar, 643
lividus, Cnemidophorus, 86, 654
lizard
collared, 721
earless, 721
mountain short-horned, 731
northern tree, 728
north plateau, 725
northern side-blotched, 730
plateau whiptail, 731
sagebrush, 722
Lonchocarpus lanceolatus, 645
longicirrus, Dasymetra, 547
longifrenis, Sibon, 201
longissimus, Oedipina, 188
loomisi, Atelopus, 189
loquax, Hyla, 212, 225, 319, 588
loreala, Hypsiglena, 737
lotor, Procyon, 441
Loxocemus
bicolor, 89, 654, 679
sumichrasti, 89
lumbricalis, Typhlops, 204
Lumbricus
rubellus, 516
terrestris, 516
lundelli,
Sceloporus, 602
Sideroxylon, 210
Lycodon
osmanhilli, 202
rufo-zonatus, 166
Lycosidae, 725, 729
lygaeid, 403
Lygaeidae, 729
Lygosoma
laterale, 396, 567
reevesii, 163
lynxe, Eumeces, 198
lyrica, Tibicen, 400

Mabuya
brachypoda, 77, 200, 246, 603, 653, 660, 679
macularia, 200
postnasalis, 200
Maclura pomifera, 505
macrolepis, Sceloporus, 201
macrophylla,
Quercus, 648
Swietenia, 210
macrostemma, Thamnophis, 117
macrotympanum,
Hyla, 320
Ptychohyla, 302, 304, 320
macularia, Mabuya, 200
maculata,
Holbrookia, 199, 398, 404, 721, 722
Leptodeira, 102, 654, 655, 656, 660, 680, 698
Megalops, 102
maculatum, Ambystoma, 516
maculiferus, Geophis, 97, 654, 669, 683, 684, 701
magna, Sturnella, 397
Magnadigita
cerroensis, 187
nigrescens, 187
pesrubra, 187
torresi, 188
Magnolia, 643
malleisi, Leptodeira, 240, 608
Malphigia mexicana, 644
mangle, Rhizophora, 649
maniculatus, Peromyscus, 401, 403, 442
manisorum, Hyla, 193
Manolepsis putnami, 104, 654, 656, 660, 679
marcianus, Thamnophis, 507, 518
margaritiferus, Drymobius, 94, 213, 239, 606, 654, 655, 656, 660, 666, 679
marinus, Bufo, 23, 215, 221, 587, 652, 656, 660, 679

marmoreus, Bufo, 23, 652, 655, 669, 679
maritima, Canavalia, 649
marsupialis, Anolis, 197
martindelcampi, Tantilla, 680
martini, Hyla, 212, 225, 588
Masticophis, 370
  australis, 104, 654
  flagellum, 397
  mentovarius, 212, 680
  spinalis, 166
  striolatus, 104, 654, 655, 663, 666, 669, 679, 686
  taeniatus, 104, 654, 660, 663, 685, 725, 728, 734
matudae, Plectrohyla, 195, 322
mayensis, Micrurus, 611
meandricus, Gobiesox, 517
megacystis, Zeugorchis, 547
Megalops maculata, 102
megalotis, Reithrodontomys, 401, 403, 442, 514
megametricum, Ochetosoma, 547
megapoda, Rana, 54, 652, 657, 660, 686, 701
melanogaster, Thamnophis, 118, 204, 655, 657, 660, 661, 685
melanoleucus, Pituophis, 403, 735, 736
melanolomus, Dryadophis, 93, 238, 606, 653, 656, 660, 666, 679, 699
melanomma, Hyla, 326, 682, 685
melanotus, Leptodactylus, 223, 587
Melanoplus
  bivittatus, 397, 400, 403
  devastator, 397, 403
  differentialis, 398, 400, 403
  femur-rubrum, 396
  mexicanus, 397, 403
  scudderi, 400, 403
melanorhinus, Sceloporus, 71, 653, 656, 662, 679
melanotus,
  Cystignathus, 30
  Leptodactylus, 30, 652, 655, 656, 660, 679
melanurus, Drymarchon, 239
melodia, Melospiza, 516
Melospiza melodia, 516
mentovarius, Masticophis, 212, 680
Mephitis mephitis, 441
meridianus, Coniophanes, 605
Mesa Verde National Park, amphibians and reptiles of, 711
Mesa Verde night snake, 737
mesquite-grassland, 12
metallica, Anadia, 196
Mexican plateau, 10
mexicana,
  Bolitoglossa, 586, 611
  Cecropia, 210
  Cedrela, 210
  Ficus, 645
mexicana—*Concluded*
  Leucopremna, 645
  Malphigia, 644
  Salvadora, 108, 655, 660, 666, 669, 679
  Terrapene, 593
mexicanus,
  Dermophis, 246
  Leptophis, 241, 608, 680, 698
  Melanoplus, 397, 403
  Spilotes, 243, 610
  Xenodon, 212, 244
  Zamenis, 108
Mexico, amphibians and reptiles from Yucatan Peninsula, 577
Michoacan
  climate, 637
    distribution of herpetofauna, 677
  geological history, 636
  geology, 632
  hydrography, 635
  origin of herpetofauna, 691
  physiography, 632
  Pleistocene biogeography, 695
  patterns of distribution of herpetofauna, 687
  vegetation, 639
michoacana,
  Pinus, 648
  Zexmenia, 646
michoacanensis,
  Contia, 109
  Elaps, 118
  Micrurus, 118, 119, 655
  Sonora, 109, 655, 689
Microbatrachylus
  albolabris, 34
  hobartsmithi, 33, 652, 657, 660, 681, 682
  imitator, 34
  minimus, 34
  persimilis, 192, 194
  pygmaeus, 34, 652, 656, 666, 682
  rearki, 194
microcephala, Hyla, 212, 225, 588, 652, 679
microeximia, Hyla, 49
microlepidotus,
  Anolis, 682, 685
  Sceloporus, 69, 653
microphylla, Bursera, 646
microstomus, Typhlops, 605
Microtus
  californicus, 397
  ochrogaster, 397, 401, 403, 514, 544
  pennsylvannicus, 396, 516
  pinetorum, 397, 401, 417
Micrurus
  affinis, 244, 611
  alienus, 611
  alleni, 202

Micrurus—*Concluded*
apiatus, 244
browni, 683, 685
distans, 118, 655, 656, 659, 660, 680, 699
elegans, 247
fitzingeri, 129
laticollaris, 119, 655, 656, 680, 699
mayensis, 611
michoacanensis, 119, 655
nigrocinctus, 680
nuchalis, 680
pachecoi, 202
richardi, 202
veraepacis, 247
Middle American tree frogs, Ptychohyla, 297
migratorius, Turus, 396
milk snake, 737
millepunctata, Cochranella, 190
milleri, Hyla, 324
Mimosa, 646
distachya, 643
pigra, 644
rosei, 644
minimus,
Eleutherodactylus, 192
Microbatrachylus, 34
minutissimus, Thorius, 189
Miogryllus verticalis, 396
miotympanum, Hyla, 323, 481
Miridae, 725, 729
mixomaculata, Hyla, 193, 342
Mocis latipes, 401
modestus, Syrrhophus, 124
moesta, Hyla, 473
mollis, Schilbeodes, 517
molossus, Crotalus, 121, 655, 657, 660, 681, 683
Monstera, 645
montanus,
Cercocarpus, 729
Reithrodontomys, 398
montezumae,
Pinus, 648
Rana, 54, 652, 657, 660, 661, 686, 701
moraviensis, Hyla, 194
moreleti,
Bolitoglossa, 215, 220, 586
Crocodylus, 215, 229, 593
morleyi, Ninia, 609
mormon, Coluber, 356, 374, 375, 376, 397, 413, 419, 420, 423, 440
mountain short-horned lizard, 731
mucronatus, Sceloporus, 682
Muhlenbergia, 646
muhlenbergii, Quercus, 505
mulleri, Bolitoglossa, 215, 220, 586
multicarinatus, Gerrhonotus, 397, 430, 665
multiplicatus,
Dermophis, 680, 698
Scaphiopus, 21, 652
multivirgatus, Eumeces, 198, 733
Murina aurata, 168
murucoides, Ipomoea, 646
Mus musculus, 397
Muscidae, 729
musculus, Mus, 397
Mustela rixosa, 396
mutabilis, Elaphe, 246
muticus, Trionyx, 196
mydas, Chelonia, 56, 590

nasus, Conopsis, 92, 654, 660, 683, 700
nasutus, Bothrops, 212, 245
National
Museum, United States, 185
Park, Mesa Verde, 713, 717
Science Foundation, 357
natricis, Kalicephalus, 164
Natrix
harteri, 203
isabelleae, 113, 655
paucimaculata, 203
rigida, 203
ruthveni, 165
sinicola, 203
sipedon, 396, 397, 401
valida, 113, 655, 660, 679
vibakari, 165
nebulata, Sibon, 243
nebulatus,
Coluber, 109
Sibon, 109, 243, 655, 679
nebulosus, Anolis, 61, 653, 655, 656, 657, 658, 659, 662, 663, 679, 686
Neduba carinata, 397
nelsoni,
Anolis, 197
Aristelliger, 197
nemanorum, Xenosaurus, 201
Nematus ribesii, 396
Nemobius fasciatus, 396
nemoralis, Coleonyx, 127, 215, 653, 679
Neoconocephalus robustus, 400
neoniger, Lasius, 725, 728, 729
Neorenifer
georgianum, 444
lateriporus, 443
septicus, 444
nereus, Typhlotriton, 189
nevermanni, Conophis, 264, 272
New Mexico milk snake, 737
new species
of frog (genus Tomodactylus) from western Mexico, 175
of turtle, genus Kinosternon, from Central America, 615
nietoi, Ninia, 246

niger, Lasius, 725, 728, 729
night snake, 737
nigrescens,
  Crotalus, 121, 655
  Magnadigita, 187
nigripes, Orchelimum, 400
nigrita, Pseudacris, 397
nigrocinctus,
  Geophis, 97, 654, 658, 660, 683, 684, 701
  Micrurus, 680
nigrofasciata, Leptodeira, 680
nigroluteus, Tretanorhinus, 244
nigromaculata, Rana, 158
nigroreticulatus, Hypopachus, 229, 589
Nimosa spirocarpa, 644
Ninia
  cerroensis, 203
  diademata, 246
  morleyi, 609
  nietoi, 246
  sebae, 241, 609
nitida, Avicenna, 649
nitidus, Tomodactylus, 40, 652, 680, 686
Noctuidae, 729
north plateau lizard, 725
northern
  side-blotched lizard, 730
  tree lizard, 728
norvegicus, Rattus, 397
Nothopsis torresi, 203
nothus, Scaphiodontophis, 609
Notropis heterolepis, 517
nuchalis, Micrurus, 680
nucifera, Cocos, 649
nummifer, Bothrops, 245
nuntius, Crotalus, 737
nutans, Sorghastrum, 505
nuttalli, Peromyscus, 396

oaxacae, Coluber, 371
obscura, Schistocerca, 400
obscurum, Lepidophyma, 199
obsoleta, Elaphe, 401, 438, 544
obsoletus,
  Coniophanes, 201
  Eumeces, 395, 402, 403
obtusata, Quercus, 648
obtusissima, Physaloptera, 444
occidentalis,
  Ameiva, 196
  Bufo, 29, 652, 657, 658, 682, 684, 686, 699
  Cnemidophorus, 83, 653
  Dermophis, 186
  Eleutherodactylus, 652, 666, 686
  Leptodactylus, 31, 652, 686
occidentale, Tropidodipsas, 113, 655, 683
occipitomaculata, Storeria, 396
Ochetosoma megametricum, 547
ochoterenai, Eumeces, 683
ochrogaster, Microtus, 397, 401, 403, 514, 544
ochrorhyncha, Hypsiglena, 102, 654
odonelli, Bolitoglossa, 586
odorata, Bursera, 646
Oedipina
  alleni, 188
  bonitaensis, 188
  cyclocauda, 188
  gracilis, 188
  inusitata, 188
  longissimus, 188
  pacificensis, 188
  serpens, 189
  syndactyla, 189
oedipine, 397
Oedipus robertsi, 19
oligantha, Aristida, 505
oligoporus, Sceloporus, 70, 653
olivacea,
  Chelonia, 125
  Gastrophryne, 402, 514
  Lepidochelys, 125
olivaceus, Sceloporus, 420, 444
Amaseus sp., 398
omiltemana, Rhadinea, 683, 685
omiltemanus,
  Anolis, 682, 685
  Geophis, 683, 685
oöcarpa, Pinus, 648
Oochoristica, 725
  bivitellobata, 728, 733
Opheodrys, 404
  blanchardi, 735
  vernalis, 396, 735
Ophidascaris, 444
ophiophthalmum, Lepidophyma, 200
Ophis colubrinus, 290
Ophisaurus attenuatus, 398, 403, 439
Opuntia, 644
orarius, Tomodactylus, 40, 652
orbiculare,
  Lacerta, 127
  Phrynosoma, 127, 681, 682
Orbigyna cohune, 210, 649
Orchelimum
  nigripes, 400
  vulgare, 400
ordinaria, Ambystoma, 15
ordinarium, Ambystoma, 15, 652, 658, 662, 682
orientalis,
  Bombina, 153
  Leposoma, 200
origin, herpetofauna of Michoacan, 691
ornata,
  Emys, 126
  Pseudemys, 126, 593, 653
  Terrapene, 720

Ornate box turtle, 720
ornatissimum, Phrynosoma, 731
ornatus, Urosaurus, 201, 720, 726, 728
Orthorrhapha, 725, 729
oryzoides, Leersia, 505
osmanhilli, Lycodon, 202
osteosperma, Juniperus, 729
Otitidae, 729
Otocoris alpestris, 397
ovata, Hicoria, 505
ovis, Hypopachus, 53
Oxybelis
  aeneus, 104, 212, 241, 609, 654, 656, 666, 679
  auratus, 104, 609, 654
  fulgidus, 609
Oxyrhophus
  aequifasciatus, 246
  petola, 246
oxyrrhinus, Hypopachus, 53, 652, 657, 660, 661, 686

pachecoi, Micrurus, 202
Pachycereus pecten-aboriginum, 644
pachyderma, Hyla, 473, 485
Pacific coastal plain, 10
pacificensis, Oedipina, 188
pacificus, Pristoceuthophilus, 397
padifolia, Ficus, 644
pallidum, Erythroxylon, 644
pallidus, Trionyx, 196
palmipes, Rana, 215, 229, 590
paludicola, Coluber, 371
palustris,
  Bolitoglossa, 187
  Rana, 397, 516
paniculata, Apoplanesia, 643, 644
Panicum virgatum, 505
parva, Cryptotis, 401, 403, 442
parvifolia, Ceiba, 645
parvisocius, Cnemidophorus, 701
parvulus, Eumeces, 80, 653, 656, 679
paucimaculata, Natrix, 203
paucituberculatus Phyllodactylus, 60, 653, 680, 701
pecten-aboriginum, Pachycereus, 644
pectinata,
  Ctenosaura, 64, 653, 655, 656, 660, 663, 679
  Cyclura, 64
Pelamis platurus, 119
pellucida, Canoula, 397
penduliflorum, Cymbopetalum, 210
pennsylvannicus,
  Gryllus, 396
  Microtus, 396, 516
pentagonus, Acanthocereus, 644
pentandra, Ceiba, 210
perixantha, Geoemyda, 58, 653
Peromyscus, 734
  leucopus, 396, 401, 403, 442, 514
  maniculatus, 401, 403, 442
  nuttalli, 396
Perosuchus fuscus, 126
perplexus, Bufo, 29, 652, 659, 680, 701
persimilis,
  Eleutherodactylus, 192, 194
  Microbatrachylus, 192, 194
pes-caprae, Ipomoea, 649
pesrubra, Magnadigita, 187
petasatus, Triprion, 212, 589
petersi,
  Geophis, 98, 654, 657, 683, 699
  Tomodactylus, 41, 652
petola, Oxyrhophus, 246
phaescens, Elaphe, 606
phaeota, Smilisca, 212, 229
Pharyngodon giganticus, 721, 725, 728, 729, 730, 733
phenops, Lepototyphlops, 89, 654, 663, 679, 701
Philodendron, 645
phoeniceus, Agelaius, 398
Phrynohyas
  corasterias, 45
  inflata, 45, 652, 660, 679
  spilomma, 212, 588
Phrynosoma
  asio, 65, 653, 679
  douglassi, 731, 734
  orbiculare, 127, 681, 682
  ornatissimum, 731
  taurus, 682, 685
Phyllodactylus
  delcampi, 680
  duellmani, 59, 653, 656, 659, 660, 662, 680, 701
  homolepidurus, 59, 653, 656, 679
  lanei, 59, 653, 656, 660, 679
  paucituberculatus, 60, 653, 680, 701
Phyllodistomum sp., 733
Phyllomedusa
  alcorni, 44
  callidryas, 212, 226, 589
  dacnicolor, 44, 189, 652, 656, 660, 662, 669, 679
  saltator, 189, 195
  tavlori, 212, 226, 589
Phyllophaga, 396, 401, 725, 728, 729
Physa anatina, 443
Physaloptera obtusissima, 444
physiography
  of Michoacan, 10, 632
  of southern El Petén, 209
picta,
  Chrysemys, 397, 405
  Hyla, 226, 588
pictus, Stenopelmatus, 397
pigra, Mimosa, 644
Pine-oak forest, 12, 647
pinetorum, Microtus, 397, 401, 417
pineus, Eumeces, 198
pinorum, Hyla, 323

Pinus
edulis, 729
hartwegi, 648
lawsoni, 648
leiophylla, 648
michoacana, 648
montezumae, 648
oöcarpa, 648
pringlei, 648
pseudostrobus, 648
pipiens, Rana, 55, 229, 394, 405, 514, 590, 652, 659, 682, 684, 685, 687, 720
pipilans, Syrrhophus, 680
Pithecoctenium echinatum, 644
Pithecollombium lanceolatum, 644
Pituophis, 725
affinis, 736
deppei, 105, 655, 657, 661, 685
deserticola, 735
intermedius, 95
lineaticollis, 105, 655, 657, 658, 683, 684, 686, 699
melanoleucus, 403, 735, 736
plagosus, Conophis, 264
plancyli, Rana, 159
Plateau
lizard, 725
whiptail lizard, 731
platura, Anguis, 119
Platyceps, 371
platyloba, Caesalpina, 644
platypterus, Buteo, 440, 544
platyrhinos, Heterodon, 397
Plectrohyla, 301, 471, 473
brachycephala, 195
crassa, 487
guatemalensis, 488
matudai, 195
Pleistocene of Michoacan, 695
plesientera, Lechriorchis, 547
Plethodon cinereus, 516
plicatus,
Alopoglossus, 196
Ptychoglossus, 196
Pliocercus
aequalis, 242
andrewsi, 609
annellatus, 203
elapoides, 246
euryzonus, 242
salvini, 246
Plumeria rubra, 645
plurifoliatum, Cercidium, 643, 644
Poa pratensis, 505
poecilonotus, Pseustes, 243
poinsetti, Sceloporus, 201
Polydelphis, 444
Polygonum, 505
polysticta,
Caudisona, 122
Leptodeira, 128, 240
polystictus, Crotalus, 122, 655, 660
polyzona, Lampropeltis, 240
pomifera, Maclura, 505
postnasalis, Mabuya, 200
postremus, Thamnophis, 117, 655
praestans, Leptophis, 241
pratensis, Poa, 505
priapus, Coluber, 371, 374, 375, 397, 413, 419, 420, 423
primus, Lechriorchis, 547
pringlei, Pinus, 648
Pristoceuthophilus pacificus, 397
proboscidea, Hyla, 194, 473
procera, Cyrtocarpa, 644
Procyon lotor, 441
Prosopis
chilensis, 644
juliflora, 643
proximans, Thamnophis, 610
pruinosa, Tibicen, 400
Prunus americanus, 505
Psammophis, 256
lineatus, 262
Pselaphidae, 729
Pseudacris
nigrita, 397
triseriata, 403, 514
Pseudemys
ornata, 215, 231, 593, 653, 679
scripta, 126, 195, 215, 231, 593, 653, 679
taylori, 195
Pseudoeurycea
altamontana, 684
belli, 17, 652, 657, 658, 660, 681, 682, 684, 690
cephalica, 684
leprosa, 684
robertsi, 19, 652, 658, 662, 682, 684
Pseudoficimia
frontalis, 105, 655, 656, 659, 699, 701
pulcherrima, 106, 655, 660, 680, 701
pseudoscorpion, 725
pseudostrobus, Pinus, 648
Pseustes poecilonotus, 243
Psyllidae, 729
Pternohyla fodiens, 44, 652, 680
Ptychoglossus plicatus, 196
Ptychohyla, 301, 303, 314, 471
adipoventris, 314, 324
bogerti, 316
chamulae, 195, 306
euthysanota, 302, 303, 304, 316
ignicolor, 303, 337
leonhardschultzei, 303, 323, 682
leonhard-schultzei, 324
macrotympanum, 302, 304, 320
matudai, 322
quecchi, 343
sagorum, 344

Ptychohyla—*Concluded*
schmidtorum, 303, 306, 331
spinipollex, 302, 303, 327
publia, Ficimia, 607, 680
pulcher,
Conophis, 274
Tomodon, 274
pulcherrima,
Emyda, 125
Geoemyda, 125, 653, 679
Pseudoficimia, 106, 655, 660, 680, 701
pullatus, Spilotes, 243, 610
punctatus,
Bufo, 719, 733
Diadophis, 92, 381, 401
pungens, Jaquinia, 644
purpurascens, Anoplarchus, 517
purpurea, Anono, 645
pusillus, Crotalus, 122, 655, 657, 658, 660, 683
pustulosa, Rana, 55, 653, 659, 664, 682
pustulosus, Engystomops, 587
putnami,
Dromicus, 104
Manolepis, 104
putorius, Spilogale, 441
pygmaeus, Microbatrachylus, 34, 652, 656, 666, 682, 700
pyrocephalus, Sceloporus, 72, 653, 655, 656, 660, 663, 666, 679, 701
Pyrus ioensis, 435

quecchi, Ptychohyla, 343
Quercus
borealis, 505
calophylla, 648
crassifolia, 648
decipiens, 648
gambelii, 724, 726
macrophylla, 648
muhlenbergii, 505
obtusata, 648
reticulata, 648
vellifera, 648
velutina, 505
quinquecarinatus, Enyaliosaurus, 701

rabdocephalus, Xenodon, 244
raccoon, 441
racemosa, Languncularia, 649
racer,
blue, 357
natural history of, 353
yellow-bellied, 357
radix, Thamnophis, 496, 518
rainforests of southern El Peten, Guatemala, 205
Rallus virginianus, 544
Rana
amurensis, 160
brachycephala, 720
catesbeiana, 397, 516
clamitans, 396, 516
coreana, 160
dunni, 54, 652, 657, 686, 701
dybowskii, 161
megapoda, 54, 652, 657, 660, 668, 701
montezumae, 54, 652, 657, 660, 661, 686, 701
nigromaculata, 158
palmipes, 215, 229, 590
palustris, 397, 516
pipiens, 55, 229, 394, 405, 514, 590, 652, 659, 682, 684, 685, 687, 720
pustulosa, 55, 653, 659, 664, 682
rugosa, 157
sierramadrensis, 682, 685
sylvatica, 396, 516
temporaria, 161
rapicaudus, Thecadactylus, 595
rattlesnake, 737
Rattus, 168
norvegicus, 397
rearki, Microbatrachylus, 194
rectiphilus, Kalicephalus, 444
redimitus, Geagras, 96, 654, 660, 663, 679, 699
red-spotted toad, 719
reevesii, Lygosoma, 163
Reevesii, Tiliqua, 163
Reithrodontomys
megalotis, 401, 403, 442, 514
montanus, 398
Renifer ellipticus, 444
reptiles
from the Yucatan Peninsula, Mexico, 577
of Mesa Verde National Park, Colorado, 711
of the rainforests of southern El Petén, Guatemala, 205
reticulata,
Cochranella, 191
Diaglena, 42, 652, 660, 679
Quercus, 648
reticulatum, Lepidophyma, 200
Review of the frogs of the Hyla bistincta group, 469
rhabdocephalus, Xenodon, 680, 698
Rhabdophis
lateralis, 164
tigrina, 164, 168
Rhadinea
aemula, 683, 685
altamontanus, 203
decipiens, 203
decorata, 246
hesperia, 106, 655, 656, 659, 663

Rhadinea—*Concluded*
laureata, 107, 655, 657, 681, 683, 684
omiltemana, 683, 685
rubricollis, 203
taeniata, 107, 655, 681, 683
rhadiphorine, 403
Rhagionidae, 725, 729
rhinolopha, Iguana, 64, 235, 599, 653
Rhinophrynus dorsalis, 20, 212, 586, 652, 660, 679, 699
Rhinotermitidae, 725
Rhizophora mangle, 649
rhodopis, Eleutherodactylus, 222
Rhus glabra, 505
Rhyacosiredon
altimirani, 684
rivularis, 684
zempoalensis, 684
ribesii, Nematus, 396
richardi, Micrurus, 202
Richmondena cardinalis, 398
rickardsi, Hyla, 319
rigida, Natrix, 203
rivularis,
Hyla, 194, 342
Rhyacosiredon, 684
rixosa, Mustela, 396
robertsi,
Pseudoeurycea, 19, 652, 658, 662, 682, 684
Oedipus, 19
robertsorum, Hyla, 473, 481
robustofemora, Hyla, 487
robustus, Neoconocephalus, 400
Rockefeller Experimental Tract, 355, 393, 496
Rocky Mountain toad, 720
rodeki, Cnemidophorus, 604
rodriguezi, Anolis, 234, 595
rosei, Mimosa, 644
rossignoni, Chelydra, 215, 230
rostralis, Eleutherodactylus, 222
rozellae, Hyla, 316
rubellus, Lumbricus, 516
rubida, Geoemyda, 58, 653, 679
rubidus, Drymarchon, 93, 654
rubra, Plumeria, 645
rubricollis, Rhadinaea, 203
rufescens, Tomodactylus, 41, 652, 658, 660, 682, 684, 702
rufioculis, Hyla, 194, 342
rufodorsata, Elaphe, 167
rufodorsatus, Tropidonotus, 167
rufozonatum, Dinodon, 166
rugosa, Rana, 157
rugulosus, Eleutherodactylus, 38, 223, 652, 656, 664, 666, 679
rupicola, Fendlera, 729
ruthveni,
Amphiesma, 165
ruthveni—*Concluded*
Lampropeltis, 102, 654, 661, 686, 701
Natrix, 165
rutiloris, Thamnophis, 610

Sabal sp., 210
sacki, Cnemidophorus, 680
sagebrush lizard, 722
sagorum, Ptychohyla, 344
sagrei, Anolis, 596
salamander, 186
tiger, 718
Salientia, 186
Salix, 646
Salmo gairdnerii, 517
saltator,
Agalychnis, 189, 195
Eleutherodactylus, 682, 685
Phyllomedusa, 189, 195
Salvadora
bairdi, 108, 655, 657, 663, 685
Bairdii, 108
lemniscata, 680
mexicana, 108, 655, 660, 666, 669, 679
salvadorensis, Hyla, 341
Salvelinus fontinalis, 517
salvini, Pliocercus, 246
sanniola, Sibon, 609
Sarcophagidae, 729
sartori,
Hyla, 124
Tropidodipsas, 247, 610
sauritus, Thamnophis, 396
saxatilis, Tomodactylus, 177, 195
scalaris,
Cnemidophorus, 86, 654, 657, 660, 685
Sceloporus, 72, 653, 661, 681, 682, 684, 686
Thamnophis, 118, 655, 662, 665, 683, 684
scaliger, Thamnophis, 118, 655
Scalopus aquaticus, 401
Scaphiodontophis
annulatus, 246
carpicinctus, 246
hondurensis, 246
nothus, 609
zeteki, 609, 612
Scaphiopus
hammondi, 21, 652, 657, 660, 685, 740
multiplicatus, 21, 652
Scarabaeidae, 725, 728
Scelionidae, 729
Sceloporus, 732
aeneus, 66, 653, 657, 658, 662, 665, 681, 682, 684, 690, 700
aquaticus, 397

Sceloporus—*Concluded*
asper, 66, 653, 667, 682, 699
bulleri, 66, 653, 658, 660, 667, 682, 690, 700
calligaster, 71, 653
chrysostictus, 601
cozumelae, 602
dugesi, 67, 653, 657, 661, 663, 667, 685
elongatus, 725
formosus, 682, 684
gadowae, 68, 653, 656, 659, 663, 680, 701
gaigeae, 602
graciosus, 398, 404, 720, 722, 726, 734
grammicus, 69, 653, 658, 660, 662, 665, 666, 681, 682, 684
heterolepis, 69, 653, 681, 682, 700
horridus, 70, 653, 655, 656, 663, 679
intermedius, 67, 653
lundelli, 602
macrolepis, 201
melanorhinus, 71, 653, 656, 662, 679
microlepidotus, 69, 653
micronatus, 682
oligoporus, 70, 653
olivaceus, 420, 448
poinsetti, 201
pyrocephalus, 72, 653, 655, 656, 660, 663, 666, 679, 701
scalaris, 72, 653, 661, 681, 682, 684, 686
siniferus, 73, 653, 655, 666
spinosus, 73, 653, 657, 660, 663, 667, 685
stejnegeri, 680
torquatus, 74, 653, 658, 662, 665, 667, 681, 682, 684, 686
undulatus, 396, 403, 720, 722, 725
utiformis, 75, 653, 656, 667, 690
yarrowi, 683
Schilbeodes mollis, 517
Schistocerca
americana, 400
obscura, 400
schistosa, Tantilla, 203, 204, 247
schlegeli, Bothrops, 201, 245
schmidti,
Anolis, 63, 653, 660, 679
Coniophanes, 605
schmidtorum, Ptychohyla, 303, 306, 331
schrencki, Elaphe, 168, 169
schwartzei, Eumeces, 236, 603, 701
Scincella, 163
assata, 77, 653, 656, 663, 679
cherriei, 199, 201, 236, 603
ixbaac, 603
Scincella—*Concluded*
lampropholis, 199, 201
taylori, 77, 653
Scoliidae, 728
scripta, Pseudemys, 126, 195, 231, 593, 653, 679
scrutator, Calosoma, 401, 442
scudderi, Melanoplus, 400, 403
scutellation of Conophis, 258
sebae, Ninia, 241, 609
Selenicereus, 645
Senecio tolucanus, 648
septentrionalis, Leptodeira, 128, 654, 679
septicus, Neorenifer, 444
sericeus, Anolis, 234, 596
serpens, Oedipina, 189
serratus, Laemanctus, 600
Sertoli syncitium, 415
sexlineatus, Cnemidophorus, 396, 398, 402, 403, 404, 420
short-horned lizard, 731
Sibon
dimidiata, 243
longifrenis, 201
nebulata, 243
nebulatus, 109, 655, 679
sanniola, 609
Sibynophis
collaris, 203
triangularis, 203
side-blotched lizard, 730
Sideroxylon
capiri, 645
lundelli, 210
Sierra de Coalcomán, 10
sierramadrensis, Rana, 682, 685
Sigmodon hispidus, 401, 544
silus, Typhlops, 204
simaruba, Bursera, 645
similis, Ctenosaura, 212, 598
simplex, Arphia, 403, 406
sinensis, Trionyx, 161
sinicola, Natrix, 203
siniferus, Sceloporus, 73, 653, 655, 666
sinistra, Ameiva, 80, 653
sipedon, Natrix, 396, 397, 401
Siredon Dumerili, 15
sirtalis, Thamnophis, 396, 398, 401, 404, 411, 665
Sistrurus catenatus, 381
skiltonianus, Eumeces, 397
skink, two-lined, 733
skunk, 441
smaragdina, Hyla, 51, 652, 657, 662, 682, 686
Smilisca
baudini, 228, 589
cyanosticta, 229
gabbi, 193
phaeota, 212, 229
wellmanorum, 194, 195

smithi, Hyla, 52, 652, 655, 656, 660, 679
snake
garter, 733
desert striped whip, 734
Great Basin gopher, 735
Mesa Verde night, 737
New Mexico milk, 737
Solidago sp., 505
Some reptiles and amphibians from Korea, 149
Sonora michoacanensis, 7, 109, 655, 659
sonorensis, Zizyphus, 643
Sorghastrum nutans, 505
southi, Leposoma, 200
spadefoot toad, 740
sphaerocarpa, Bursera, 644
sparrow hawk, 441
sparverius, Falco, 440, 544
speciation of herpetofauna in southwestern Mexico, 700
speckled earless lizard, 721
Spelerpes belli, 17
Spermophilus, 416
Sphaerodactylus
glaucus, 594
lineolatus, 232
sphingid, 516
Spilogale putorius, 441
spilomma, Phrynohyas, 212, 588
Spilotes
mexicanus, 243, 610
pullatus, 243, 610
spinalis,
Coluber, 371
Masticophis, 166
Zamenis, 166
spinifera, Trionyx, 196
spinipollex, Ptychohyla, 302, 303, 327
spinosa, Centrolenella, 190, 195
spinosus, Sceloporus, 73, 653, 657, 660, 663, 667, 685
spirocarpa, Nimosa, 644
splendida, Leptodeira, 103, 654, 659, 680, 699
stansburiana, Uta, 720, 726, 730
Staphylinidae, 729
staufferi, Hyla, 194, 212, 226, 588, 680, 698
Staurotypus triporcatus, 215, 231, 592
Steiroxys, 397
stejnegeri, Sceloporus, 680
stejnegerianus, Coluber, 372, 374, 375, 397, 413, 419, 420, 423, 435, 440
Stenopelmatus
fuscus, 397
pictus, 397
Stenorrhina
degenhardti, 243
freminvilli, 610, 680, 698
Storeria
dekayi, 397, 517
occipitomaculata, 396
storerioides, 113, 655, 657, 658, 660, 681, 683, 684, 699
storerioides,
Storeria, 113, 655, 657, 658, 660, 681, 683, 684, 699
Tropidoclonion, 113
streckeri, Ficimia, 202
striata, Lespedeza, 505
striatus, Tamias, 397, 516, 545
striolatus,
Coluber, 104
Masticophis, 104, 654, 655, 663, 666, 669, 679, 686
striped whip snake, 734
stuarti, Dryadophis, 93
sturnella magna, 397
subcarinata, Thamnophis, 117
subcaudals, 360
subocularis, Anolis, 680
sumichrasti,
Eumeces, 236
Hyla, 322
Loxocemus, 89
supraciliaris, Bothrops, 201
suspectum, Heloderma, 194
swainsoni, Buteo, 544
Swietenia, 645
macrophylla, 210
sylvilagi, Trombicula, 442
Sylvilagus floridanus, 397, 401, 544
sylvatica, Rana, 396, 516
Synaptomys cooperi, 397
syndactyla, Oedipina, 189
syntomentera, Zeugorchis, 547
syntomenteroides, Zeugorchis, 547
Syrrhophus
leprus, 215, 223
modestus, 124
pipilans, 680

Tabebuia, 645
Tachinidae, 728
Tachydromus
amurensis, 162
wolteri, 163
Wolteri, 163
Tachymenes, 256
Tachymenis lineata, 267
taeniata, Rhadinea, 107, 655, 681, 683
taeniatus,
Dromicus, 107
Masticophis, 104, 654, 660, 663, 685, 725, 728, 734
talamancae, Cochranella, 191
Tamias striatus, 397, 516, 545
Tantilla
bocourti, 110, 655, 681, 683, 684
calamarina, 110, 655, 660, 680
canula, 610

Tantilla—*Concluded*
coronadoi, 683, 685
costaricensis, 203
cuniculator, 610
deppei, 683
martindelcampi, 680
schistosa, 203, 204, 247
taylori, 204
tapeworm, 725, 728
tarascae, Geophis, 98, 654, 669, 683, 684, 701
tau, Trimorphodon, 112, 655, 657, 660, 661, 666, 685
taurus,
Eleutherodactylus, 192
Phrynosoma, 682, 685
taylori,
Anolis, 680
Eumeces, 198
Lampropeltis, 202
Leiolopisma, 77
Phyllomedusa, 212, 226, 589
Pseudemys, 195
Scincella, 77, 653, 656, 663, 679
Tantilla, 204
Taxodium, 646
tecpanensis, Geatractus, 654, 679
temporaria, Rana, 161
Tenebrionidae, 725, 728, 729
tenuissima, Dipsas, 201
tenuissimus, Imantodes, 607
Teratohyla spinosa, 190, 195
Terrapene
carolina, 396, 405
mexicana, 593
ornata, 720
yucatana, 593
terrestris,
Bufo, 397
Lumbricus, 516
Thamnophis, 438
texana, Geckobiella, 725, 728
Thamnophis, 725
annectens, 503
brachystoma, 507, 518
butleri, 507, 518
canescens, 118, 655
chihuahuaensis, 204
chrysocephalus, 683
concinnus, 503
cyclides, 114, 117, 655
cyrtopsis, 114, 117, 507, 518
dorsalis, 117, 655, 657, 658, 659, 666, 681, 683, 684, 699
elegans, 438, 733
eques, 117, 655, 657, 661, 685
fitchi, 503
macrostemma, 117
marcianus, 507, 518
melanogaster, 118, 204, 655, 657, 660, 661, 685
ornatus, 503
Thamnophis—*Concluded*
pallidula, 503
parietalis, 502
pickeringi, 502
postremus, 117, 655
proximans, 610
proximus, 496, 518
rutiloris, 610
sauritus, 396
scalaris, 118, 655, 662, 665, 683, 684
scaliger, 118, 655
semifasciata, 502
sirtalis, 396, 398, 401, 404, 411, 495, 502, 665
terrestris, 438
tetrataenia, 503
vagrans, 733
vicinus, 115
Thecadactylus rapicaudus, 232, 595
Therevidae, 729
Thomomys, 416
Thorius minutissimus, 189
Thysanoptera, 729
Tibicen, 396
lyrica, 400
pruinosa, 400
tiger salamander, 718
tigrina, Rhabdophis, 164, 168
tigrinum, Ambystoma, 17, 652, 660, 661, 685, 718
Tilia, 643
tiliaceus, Hibiscus, 649
Tiliqua Reevesii, 163
Tingidae, 729
Tiphiidae, 728
tipulid, 516
toad,
Hammond's spadefoot, 740
red-spotted, 719
Rocky Mountain, 720
Toluca
conica, 683
frontalis, 105
lineata, 110, 654, 657, 658, 660, 683, 684
tolucanus, Sencio, 648
Tomodon, 255
lineatum, 262, 267, 277
pulcher, 274
Tomodactylus
albilabris, 682, 685
amulae, 40
angustidigitorum, 39, 652, 657, 660, 682, 684, 686, 701
dilatus, 682, 685, 701
fuscus, 39, 652, 660, 682, 684
grandis, 684
new species from western Mexico, 175
nitidus, 42, 652, 680, 686
orarius, 40, 652

Tomodactylus—*Concluded*
petersi, 40, 652
rufescens, 41, 652, 658, 660, 682, 684, 702
saxatilis, 177, 195
torquata,
Hypsiglena, 100, 102, 654, 657, 659, 680, 685, 699, 737
Leptodeira, 100
torquatus, Sceloporus, 74, 653, 658, 662, 665, 667, 681, 682, 684, 686
torresi,
Magnadigita, 188
Nothopsis, 203
transversus, Crotalus, 683
traps, for snakes, 359
Tree frogs of the genus Ptychohyla, 297
trematodes, 733
Tretanorhinus
lateralis, 244
nigroluteus, 244
triacanthos, Gleditsia, 505
triangularis, Sibynophis, 203
triaspis, Elaphe, 95, 246, 607
Trichilia hirta, 645
Trichoptera, 729
tridactylum, Bipes, 680
tridentata, Artemisia, 724
trifida, Ambrosia, 505
Trimerotropus, 397
Trimorphodon
biscutata, 111
biscutatus, 111, 655, 656, 660, 679
latifascia, 111, 655, 656, 659, 680, 699
tau, 112, 655, 657, 660, 661, 666, 685
Trionyx
ater, 195
calvatus, 196
muticus, 196
pallidus, 196
sinensis, 161
spinifer, 161
Triodopsis, 516
triporcatus, Staurotypus, 592
Triprion petasatus, 212, 589
triseriata, Pseudacris, 403, 514
triseriatus, Crotalus, 122, 655, 657, 662, 665, 681, 683, 684, 686
trivolvis, Heliosoma, 443
Trombicula
alfreddugèsi, 442, 547, 725, 728
kansensis, 442, 547
lipovskyana, 442, 547
sylvilagi, 442
Tropical semi-deciduous forest, 12, 644
Tropidoclonion
annectens, 204
Tropidoclonion—*Concluded*
lineatum, 204
storerioides, 113
Tropidodipsas
fasciata, 129, 610
occidentala, 113, 655, 683
sartori, 247, 610
tropidonotus, Anolis, 212, 597
Tropidonotus
lateralis, 164
rufodorsatus, 167
tryxaline, 397
tuberculata, Uta, 75
tuberculatus, Urosaurus, 75
Turdus migratorius, 396
turtle, box, 720
two-lined skink, 733
tygarti, Lechriorchis, 547
Type specimens of amphibians and reptiles in the Museum of Natural History, University of Kansas, 183
Typhlops
braminus, 88, 654
lumbricalis, 204
microstomus, 605
silus, 204
Typhlotriton nereus, 189
Tyto alba, 440
tzabcan, Crotalus, 611

ulmifolia, Guazuma, 644
undulata, Ameiva, 80, 212, 603, 653, 656, 660, 666, 679
undulatus,
Bothrops, 683
Sceloporus, 396, 403, 720, 722, 725
unicolor, Enulius, 95, 654, 656, 663, 683, 684
uniformis, Anolis, 595, 612
uranochroa, Hyla, 342
Uropsophys triseriatus, 123
Urosaurus
bicarinatus, 75, 653, 679, 686
caeruleus, 201
gadowi, 76, 653, 663, 680, 701
ornatus, 201, 720, 726, 728
tuberculatus, 75, 653
wrighti, 728
urosteges, 360
usta, Gastrophryne, 124, 652, 679
ustus, Anolis, 596
Uta
caerulea, 201
gadovi, 76
stansburiana, 720, 726, 730
tuberculata, 75
Utah tiger salamander, 718
utahense, Ambystoma, 718
utahensis, Amelanchier, 729
utiformis, Sceloporus, 75, 653, 656, 667
uvifera, coccoloba, 645

vagrans, Thamnophis, 733
valida, Natrix, 113, 655, 660, 679
valliceps, Bufo, 221, 587
varius, Atelopus, 190
vegetation
of Michoacan, 639
of southern El Petén, 209
velasci, Ambystoma, 17, 652
vellifera, Quercus, 648
velox, Cnemidophorus, 731
velutina, Quercus, 505
veracrucis, Bolitoglossa, 187
veraepacis, Micrurus, 247
vernalis,
Liopeltis, 396
Opheodrys, 396, 735
versicolor, Hyla, 397
verticalis, Miogryllus, 396
Vespidae, 728
vibakari,
Amphiesma, 165
Natrix, 165
vicinus,
Camponotus, 725, 728, 729
Thamnophis, 114
viminalis, Astianthus, 645
vinitor, Dendrophidion, 246
Vipera berus, 665
virescens, Butorides, 546
virgatum, Panicum, 505
virginianus, Rallus, 544
viridifasciata, Chortophaga, 397, 398, 400
viridis, Crotalus, 737
viridissima, Cochranella, 682, 684
viscida, Arctostaphylos, 435
vittatus,
Basiliscus, 64, 597, 653, 655, 656, 664
Conophis, 91, 277, 654, 679
Vitex sp., 210
vivipara, Lacerta, 665
vocalis, Eleutherodactylus, 38, 652
vocator, Eleutherodactylus, 192
vole, 396
vulgare, Orchelimum, 400

wandering garter snake, 733
walkeri, Hyla, 322
Webb, Robert G.
A new species of frog (genus Tomodactylus) from western Mexico, 175
Webb, Robert G., Jones, J. Knox, Jr., and Byers, George W.
Some reptiles and amphibians from Korea, 149
Wellman, John
A revision of snakes of the genus Conophis (family Colubridae) from Middle America, 253
wellmanorum,
Hyla, 194, 195
Smilisca, 194, 195
western
leopard frog, 720
Mexico, a new species of frog (genus Tomodactylus), 175
weyerae, Hyla, 194
whip snake, 734
whiptail lizard, 731
wolteri, Tachydromus, 163
woodhousei, Bufo, 514, 720
woodi, Anolis, 197
woodland biome, Mesa Verde, 713
wrighti, Urosaurus, 728

Xalapensis, Arbutus, 648
Xenodon
colubrinus, 290
mexicanus, 244
rabdocephalus, 244
rhabdocephalus, 680, 698
Xenodontinae, 255
Xenosaurus nemanorum, 201
Xiphigaster atropurpureus, 517

yarrowi, Sceloporus, 683
yellow-headed collared lizard, 721
Yucatan Peninsula, Mexico, amphibians and reptiles of, 577
yucatana, Terrapene, 593
yucatanensis, Leptodeira, 608
yucatensis, Bothrops, 611

Zamenis
mexicanus, 108
spinalis, 166
zapote, Achras, 210
zeledoni, Geophis, 202
zempoalensis, Rhyacosiredon, 684
zeteki, Scaphiodontophis, 609, 612
Zeugorchis
aequatus, 547
curinus, 547
megacystis, 547
syntomentera, 547
syntomenteroides, 547
Zexmenia michoacana, 646
Zizyphus sonorensis, 643
zweifeli, Cnemidophorus, 83, 654

31-4589

3 2044 093 361 475